Is There a Role for Top-Down Factors in ‘Automatic’ Imitation?

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List of Abbreviations

RT(s)	Reaction time(s)
ASC	Autism spectrum condition
MNS	Mirror neuron system
MN(s)	Mirror neuron(s)
AIM	Active intermodal mapping
IM	Ideomotor theory
ASL	Associative sequence learning
GOADI	Goal-directed theory of imitation
IFG	Inferior frontal gyrus
IPL	Inferior parietal lobule
STS	Superior temporal sulcus
mPFC	Medial prefrontal cortex
M1	Primary motor cortex
(r)TPJ	(Right) temporoparietal junction
STORM	Social top-down response modulation
EMG	Electromyography
(r)TMS	(Repetitive) transcranial magnetic stimulation
MEP(s)	Motor evoked potential(s)
MEG	Magnetoencephalography
PET	Positron emission tomography
fMRI	Functional magnetic resonance imaging
BOLD	Bold oxygen dependent level
ToM	Theory of Mind
SRC	Stimulus response compatibility
SOA	Stimulus onset asynchrony
ELI	Edinburgh Laterality Inventory
EQ	Empathy quotient
AQ	Autism spectrum quotient
QMME	Questionnaire of emotional empathy
IRI	Interpersonal reactivity index
ANOVA	Analysis of variance
SE	Standard error
SD	Standard deviation

Abstract

The passive perception of irrelevant actions can facilitate or interfere with the execution of one's own actions, known as 'automatic imitation' (AI). For example, when one is pressing down on a button, reaction times (RTs) are faster when observing a finger depression (compatible action) and slower whilst observing a finger lift (incompatible action). This phenomenon has been attributed to the mirror neuron system and is thought to represent a laboratory model of spontaneous motor mimicry which facilitates social interactions. AI is typically reduced or absent when the observed movement is produced by a non-human agent. However, previous findings suggest that the magnitude of this 'human bias' can be modulated by top-down factors, such as attention and prior instructions regarding whether the movement was produced by a human or non-human agent. This thesis aimed to further examine the role of attention and belief regarding stimulus agency in automatic imitation.

Participants were required to perform a pre-specified key press or release response to a diffuse yellow flash go signal. This response was either compatible or incompatible with the finger or object movement, which was presented simultaneously. AI was measured by subtracting compatible from incompatible RTs to calculate the compatibility effect.

Experiments 1a, 1b, 2 and 7 focused on exploring the role of attention in AI. Experiment 1a revealed that the human bias is dependent on *when* the go signal occurs. AI was greater for the finger stimulus relative to the object stimulus when the go signal occurred during the movement, but not after the movement. It is suggested that attention to the movement is reduced when the go signal occurs after the movement. This implies that the human bias in AI is dependent on attention being directed towards the movement. Experiments 1b and 2 indicated that AI was removed if a *visual* dual task was added, but that AI remained and was greater when an *auditory* dual task was added. This indicates that AI was removed when the visual dual task competed for cognitive resources with action observation. The facilitation of AI when an auditory dual task was added suggests that the additional cognitive load may have occupied cognitive resources required for the inhibition of imitation. These findings highlight that AI is susceptible to attentional load, implying that AI is not a strongly automatic process. Experiment 7 explored whether the spread of attention modulates the magnitude of AI by comparing a 'diffuse' go signal to a 'focused' go signal which directed attention to the stimulus movement. Significantly larger AI effects were produced for the group of participants who saw the focused flash first, indicating that focusing attention on the spatial location of the movement increased AI, and furthermore that initially observing the focused flash 'trained' participants to pay attention to the stimulus movement in the diffuse flash condition.

Experiments 3 and 4 examined why AI effects for non-human stimuli are more likely to be significant when trials are presented in separate blocks (e.g. human vs. non-human stimuli) as opposed to randomly mixed trials. It was hypothesised that this pattern of previous results could be due to less attention being drawn to stimulus differences when stimuli are presented separately as opposed to mixed with a block of trials. However, in both experiments, AI effects were present for the object stimulus in the group of participants who observed the block of finger trials first. This suggests that the prior observation of the finger movement caused a carry-over of human agency to the object stimulus. Experiments 5, 6, 8 and 9 directly explored the role of belief regarding stimulus agency in AI by instructing participants that the object movement was generated by a human finger movement. Experiments 5, 6 and 8 provided preliminary evidence that AI is affected by belief instructions, but the effects were weak or confounded by spatial stimulus-response compatibility (SRC) effects (i.e. compatibility effects based on spatial correspondence of the stimulus and response location). Experiment 9 was designed to differentiate imitative compatibility from SRC effects, thus providing a pure measure of imitative compatibility. Imitative compatibility was present for the object stimulus after the belief manipulation. This demonstrates that a human belief regarding stimulus agency of the object modulated imitative compatibility effects due to the top-down knowledge that the movement was human generated, and not due to increased attention and SRC effects.

The presented work has provided multiple lines of evidence which demonstrate that so-called 'automatic' imitation effects are strongly susceptible to top-down influences, including attention and belief regarding stimulus agency. The current work could be used to evaluate top-down modulation of imitation in autistic populations, as it has been proposed that top-down modulation of the automatic imitation pathway may be atypical in autism.

Declaration

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This thesis is dedicated to my parents John and Chona Evans, and my fiancé Danny Bolton.

Chapter One

General Introduction

1.1 Overview

What is imitation? While the answer to this question is intuitively known, the term ‘imitation’ has many possible definitions, and clear-cut definitions of the various different types of imitation have not been agreed. Possible categorisations of imitation can be found in **Table 1**, and will be used in this thesis. Broadly speaking, imitation refers to the ability to transform visual information of an observed action into one’s own reproduction of that observed action.

On the surface, imitation may appear to be a relatively low level, cognitively undemanding form of behaviour. However, there is a wide consensus that imitation is actually an advanced capability, which is linked with forms of intelligence that are characteristically human in nature such as understanding the minds of others (Meltzoff and Gopnik, 1993). As a fundamental aspect of human behaviour, the human capacity for imitation has been extensively researched across multiple disciplines. Imitation is an important mechanism as it underpins the learning of language (Arbib, 2002) and acquisition of novel technical skills and behaviours (Tomasello, 1999) without the time-consuming process of learning independently through trial-and-error. For this reason, a large proportion of human learning is achieved through observation and imitation throughout development.

Imitation is also a powerful form of social learning, essential for the development of social and communicative skills (Uzgiris, 1981), such as facial and body gestures; as well as the transfer of cultural knowledge (Tomasello et al., 1993). The ability to imitate is particularly crucial given that humans live in highly complex cultures and societies, and are required to navigate intricate social interactions. Whenever one is in an unfamiliar environment or situation, the need to rapidly learn through imitation, profiting from the observing the example of others becomes apparent. For example, when visiting a foreign culture, imitating the customs and behaviours of natives allows one to conform to the social norms of that culture.

Table 1: Definitions of the various 'types' of imitation.

Voluntary or intentional Imitation		**Involuntary or unintentional Imitation**	
'True' Imitation	The intentional reproduction of 'a novel or otherwise improbable act, or an act for which there is no instinctive tendency.' (Thorpe, 1963). Involves reproduction of an action, in which the exact kinematic features of an action are also replicated.	**Motor Mimicry**	Unintentional pro-social matching/mimicry of the behaviours of others which occurs on a non-conscious level during social interactions.
Emulation	Matching of the 'result' or 'goal' of a particular action, but not the specific kinematic features by which the goal is achieved - also known as 'goal emulation' (Tomasello and Call, 1997).	**Automatic imitation**	A type of stimulus-response compatibility effect in which the observation of a task-irrelevant action facilitates the performance of compatible actions and interferes with the performance of incompatible actions in a laboratory setting.
		Mirror effects	Measurable neurophysiological effects which occur when participants passively observe actions in a laboratory setting.
Internal state imitation			
Emotional contagion	'A process in which a person influences the emotions or behaviour of another person through the conscious or unconscious induction of emotional states and behavioural attitudes.' (Barsade, 2002). Some contend emotional contagion may represent motor mimicry, and synchronization of one's actions with those of others might cause the convergence of emotions (Hatfield et al., 1993).		

So far imitation where actions are imitated voluntarily (i.e. in situations where one consciously decides to imitate) has been discussed. However, imitation does not necessarily occur on a conscious level. Humans often imitate unintentionally without realising it, demonstrating that imitation can occur relatively automatically. Behavioural studies as far back as Darwin (1871) have recognised that there is a natural tendency to unconsciously mimic the body gestures and postures, facial expressions, mannerisms and speech patterns of an interacting partner during social interactions (Chartrand and Bargh, 1999). For example, when two people are interacting it is common to adopt the interacting partner's incidental gestures, such as ear touching and foot shaking (Chartrand and Bargh, 1999). This imitation of the non-verbal display of another person is termed 'motor mimicry' **(Table 1)**. Motor mimicry occurs automatically and without conscious awareness, and therefore constitutes a form of ‘involuntary’ or ‘unintentional’ imitation. Controlled studies in semi-naturalistic settings have shown when the experimenter intentionally copied the mannerisms of the subjects, the subjects tended to describe the interaction as smoother and more harmonious and subsequently reported that they ‘liked’ the experimenter more (Chartrand and Bargh, 1999). Thus, motor mimicry has a powerful effect in facilitating social interactions and interpersonal bonding, promoting a sense of affiliation among interacting partners (Dijksterhuis and Bargh, 2001; van Baaren et al., 2009). On this basis been argued that such mimicry may have evolved to function as a ‘social glue’ (Lakin et al., 2003). By synchronising the non-verbal behaviours of interacting partners, motor mimicry contributes to shared feelings of empathy and rapport, leading to emotional convergence. It is therefore of critical importance to establishing harmonious social interactions.

Nonetheless, such imitative tendencies must be controlled, as it would be maladaptive to be uncontrollably imitating actions in one’s social environment which are not behaviourally relevant. Accumulating evidence suggests that mimicry is subtly and sophisticatedly modulated by a number of factors, such as social attitudes (Likowski et al., 2008), social status (Cheng and Chartrand, 2003) and attractiveness (van Leeuwen et al., 2009b). These findings suggest that although mimicry occurs unintentionally and without conscious awareness, the tendency to imitate can be controlled based on social signals such as the specific goals of the interaction (van Baaren et al., 2009).

Similar effects of passive action observation on action execution have been observed in a laboratory setting. For example, studies directly measuring the electrical activity of muscles using electromyography (EMG) have shown that passively observing an action activates the specific muscles involved in performing that action, termed ‘mirror effects’ **(Table 1)**. For example, increased EMG activity has been recorded in the muscles of the arms of participants observing arm wrestling (Berger and Hadley, 1975). Similarly, behavioural studies using simple movements have demonstrated that the passive observation of an action can automatically prime the execution of that action, such that reaction times (RTs) are shorter while observing similar actions and are longer while observing different actions, termed ‘automatic imitation’ (Brass et al., 2001a) **(Table 1)**. It is widely believed that motor mimicry and automatic imitation are actually the same psychological phenomenon, the former representing the effect ‘in the wild’ (Heyes, 2011) and the latter representing the effect generated under tightly controlled experimental conditions. Furthermore, in line with observations that mimicry can be modulated by social signals, converging evidence indicates that automatic imitation effects are modulated by top-down processes, such as social priming **(section 1.7.1)**, attention **(section1.7.2)** and belief **(section 1.7.3).**

Given the importance of mimicry in social interactions, understanding the neural mechanisms that control imitation might be beneficial in understanding the social and behavioural deficits that characterise autism spectrum condition (ASC). Studies have shown that individuals with autism spectrum conditions (ASCs) perform poorly in a range of imitation tasks (Rogers and Pennington, 1991). It is also widely believed that a subset of neurons in the brain which discharge during both action execution and action observation, known as ‘mirror neurons’ (MNs), constitute the neural substrate for human imitation. A somewhat simplistic hypothesis has therefore been proposed suggesting that atypical imitation in ASC could be due to a dysfunctional mirror neuron system (MNS) (Iacoboni and Dapretto, 2006; Ramachandran and Oberman, 2006), known as the ‘broken mirror theory’ of ASC. However, evidence that autistic individuals are not impaired in explicit, goal-directed imitation (Aldridge et al., 2000; Carpenter et al., 2001; Hamilton et al., 2007) and have an intact ‘automatic imitation’ effect (Bird et al., 2007; Gowen et al., 2008; Press et al., 2010) suggests that the straightforward account provided by broken mirror theorists cannot provide a complete explanation (see Southgate and Hamilton (2008) for a review of the evidence challenging the broken mirror theory).

These findings can be reconciled by emerging evidence that modulation of automatic imitation involves a complex interplay between bottom-up (i.e. visual input regarding stimulus shape and surface characteristics) and top-down factors (i.e. prior knowledge, attention and belief). For example, automatic imitation is reduced or absent when the stimulus has a non-human form, such as a robot (Press et al., 2005; Kilner et al., 2003), suggesting a role for bottom-up factors. However, automatic imitation is also reduced when the subject is instructed that a stimulus is not human (Liepelt and Brass, 2010; Longo and Bertenthal, 2009), suggesting a role for top-down factors. The fact that prior knowledge regarding stimulus agency can influence the extent to which one automatically imitates suggests that ‘automatic’ imitation is not as automatic as first envisaged, but rather that automatic imitation requires cognitive control. These findings have led to the development of an alternative hypothesis which posits that while the neural pathway responsible for automatic imitation may be intact in ASC, top-down modulation of the automatic imitation pathway may be atypical (Hamilton, 2008).

Many researchers have primarily focussed on voluntary imitation to investigate the integrity of the MNS in conditions in which imitative capabilities are known to be impaired, such as ASC. Voluntary imitation is an extremely complex behaviour, requiring the integration of a number of brain systems (i.e. visual, motor and memory systems). Therefore, as pointed out by Bird and colleagues (2007), it is extremely difficult to determine to what extent imitative impairments in ASC are due to the impairments of the MNS, and to what extent they are due to impairments of other brain systems. For example, in such studies, participants are instructed to copy an action however the exact features of the action to be reproduced are not specified. Participants must therefore rely on the intuitive ability to read social and communicative cues and the ability to interpret the mental state of the experimenter. Given that impairments in these functions have been documented in ASC (Bird et al., 2006; Baron-Cohen et al., 1985; Abell et al., 2000) it is not clear to what extent impairments in other systems, as opposed to imitative systems, might contribute to poor imitative performance in voluntary imitation tasks. Importantly, automatic imitation tasks minimize the demands from other brain systems relative to voluntary imitation tasks (Bird et al., 2007). It can therefore be argued that simple automatic imitation paradigms provide a cleaner measure of MNS function and imitative abilities, particularly in ASCs, than complex voluntary imitation tasks. For this reason, the current work focuses on automatic imitation.

With these broader implications in mind, the current work aimed to further our understanding of the role of top-down factors in modulating automatic imitation in healthy, 'neurotypical' individuals. The term 'neurotypical' refers to individuals who are not on the autism spectrum, and do not have a history of neurological or psychological illness. A greater understanding of the influence of top-down factors in controlling imitative tendencies in neurotypical individuals will allow us to develop future experiments directly testing the top-down modulation hypothesis in ASC.

In the following sections, automatic imitation has been defined in detail, and the various automatic imitation paradigms which have been developed have been described. The main cognitive models and the neural mechanisms which have been proposed to underpin imitation have then been outlined. Recent studies which provide convincing evidence that both bottom-up and top-down processes modulate the magnitude of automatic imitation effects have then been discussed in detail. Subsequently the current theoretical models of automatic imitation have been described, and the hypothesis that top-down modulation of automatic imitation may be atypical in ASCs has been discussed. Finally, the aims and objectives of the current thesis have been outlined.

1.2 Automatic imitation

Automatic imitation paradigms provide a method of studying the spontaneous motor mimicry observed in naturalistic social interactions under tightly controlled experimental conditions (see Heyes (2011) for a recent review on automatic imitation). In a typical automatic imitation paradigm a simple action is presented, and participants are concurrently required to perform a pre-specified response in response to a separate go signal. For this reason, the presented action can be considered irrelevant to the participant's ongoing task. Nonetheless, the features of the simultaneously presented task-irrelevant action facilitate compatible actions and interfere with incompatible actions. For example, if one observes a video clip of a compatible action, such as an index finger elevation whilst required to lift one's own index finger **(Figure 1a)**, RTs tend to be faster, termed 'facilitation'. Conversely, if one watches a video clip of an incompatible action, such as an index finger depression whilst required to lift one's own index finger, RTs tend to be slower, termed 'interference'. The automatic imitation task consequently allows one to examine the effect of observing another person's action due to the fact the observer is required to simultaneously perform an action (i.e. if they were not required to move, an effect would not be produced). Performance in automatic imitation tasks is measured in terms of speed and accuracy (i.e. RT and errors incurred). The difference between RTs for compatible and incompatible trials is termed the ‘compatibility effect’, which can be used as a measure of the magnitude of automatic imitation. This phenomenon has been given a variety of names by different scholars over the years, including ‘movement compatibility’ (Brass et al., 2000) ‘imitation inhibition’ (Spengler et al., 2010a), ‘movement interference’ (Kilner et al., 2007) and ‘visuomotor priming’ (Gowen et al., 2010), however the term ‘automatic imitation’ is in common use (Heyes, 2011; Press et al., 2005; Bird et al., 2007).

The first study of automatic imitation was conducted by Stürmer and colleagues (2000). Participants were to required ‘close the hand’ (making a fist) in response to a red go signal or ‘open the hand’ in response to a blue go signal. Concurrently, hand opening and closing actions were presented. They found that the irrelevant observed movement caused faster RTs when participants performed a movement that was compatible with the observed movement, and slower RTs when they performed an incompatible movement. This effect was later replicated using an index finger movement paradigm, as described above (Brass et al., 2001a). In these paradigms, the effect is produced by compatibility between the type of movement i.e. opening/closing or tapping/lifting. They are therefore referred to as ‘movement compatibility’ automatic imitation paradigms **(Figure 1a)**.

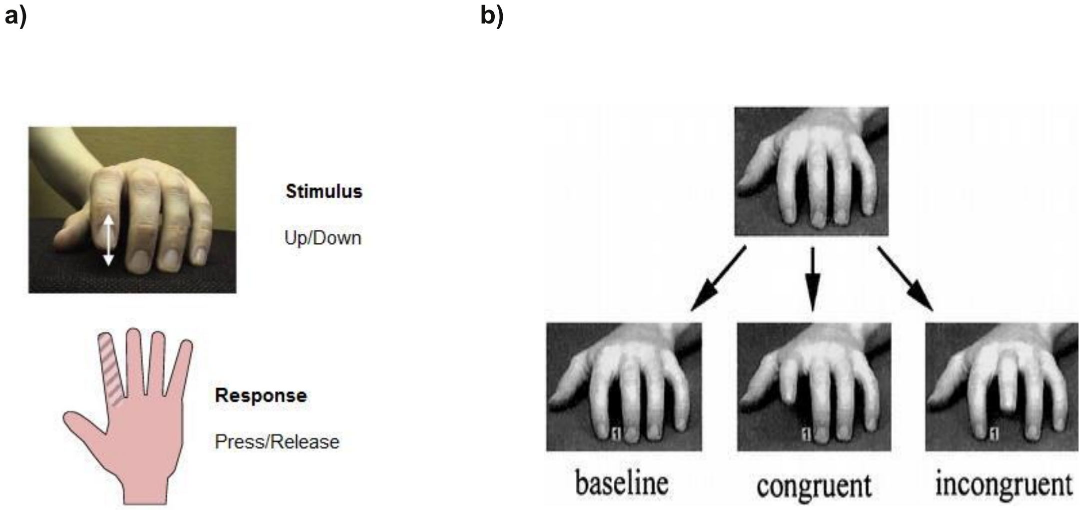

Figure 1: a) Automatic imitation movement compatibility paradigm (Gowen et al., 2010); **b)** Automatic imitation effector compatibility paradigm: the number indicates the finger to lift; here number 1 indicates a finger lift (Brass et al., 2003).

Other groups have found a similar automatic imitation effect in ‘effector compatibility’ automatic imitation paradigms, in which the compatibility effect is dependent on anatomical correspondence between the effector observed moving and the effector used to perform the action **(Figure 1b)**. While in the movement compatibility paradigm the response is pre-specified, effector compatibility paradigms typically involve a choice task, in which their response is determined by the stimulus or other go signal. For example, in the study of Brass et al. (2000), participants observed a human hand with fingers curled downwards resting on a table. When the go signal (number 1 or 2) appeared participants were required to lift the index (number 1) or middle finger (number 2) **(Figure 1b)**. The appearance of the number coincided with the lifting of either the index finger or the middle finger of the stimulus hand. They found that although the observed action was 'task irrelevant' (as the number provided the information regarding which finger to lift), participants' RTs were faster in compatible trials in which the stimulus hand moved the same finger that the participant was required to lift. Conversely, RTs were slower in incompatible trials where the stimulus hand lifted the index finger, while the participant was required to lift the middle finger or vice versa.

In theory, the difference between RTs for compatible and incompatible trials may be driven entirely by facilitation of imitatively compatible trials. By including a 'baseline' condition in which the task relevant go signal is presented in the absence of a task irrelevant movement stimulus (i.e. a static stimulus in a neutral position) **(Figure 1b)**, a number of groups have demonstrated RTs are slower in imitatively incompatible trials compared to 'baseline' trials (Brass et al., 2000; Bertenthal et al., 2006; Gillmeister et al., 2008). This suggests that, as would be expected from automatic response activation, the effect is due not only to the facilitation of imitatively compatible responses, but also due in part to interference of imitatively incompatible responses. Given that the irrelevant movement does not need to be processed to perform the relevant task successfully, and the fact that incompatible actions interfere with performance, it is inferred that the process is 'automatic'. That is to say, the automatic activation of the imitative response causes the RT advantage in imitatively compatible trials, while slower RTs on imitatively incompatible trials are due to overcoming the automatic activation of the imitative response.

Since these seminal studies, this effect has been replicated repeatedly, demonstrating that automatic imitation is a robust effect. A variety of different effectors and pairs of actions have now been examined, including finger movements (Brass et al., 2001a; Bertenthal et al., 2006; Heyes et al., 2005; Press et al., 2008; Gowen et al., 2010; Spengler et al., 2010a), hand movements (Heyes et al., 2005; Press et al., 2008; Stürmer et al., 2000), arm movements (Gowen et al., 2008; Stanley et al., 2007; Kilner et al., 2007), hand/foot movements (Bach et al., 2007) and hand/mouth movements (Leighton and Heyes, 2010). Importantly, converging evidence is beginning to support the idea that automatic imitation and motor mimicry are related effects. For example, the magnitude of automatic imitation effects have been shown to be modulated by social attitudes (Cook and Bird, 2011), providing indirect evidence that automatic imitation and mimicry might reflect the same psychological process. The exact neural mechanism which generates such automatic imitation effects (and other types of imitation) is currently unknown. However, a number of theories have been proposed to answer this question, which will be discussed in the following sections.

1.3 Theories of imitation

Although imitation has been a topic of intense research, the neural underpinnings and mechanisms at the core of imitation are still not fully understood. The fundamental question of how visual perception-to-motor mapping is achieved is often referred to as the ‘correspondence problem’ (Heyes, 2001). In order to solve the correspondence problem one must translate visual information from a modelled action to generate a matching motor output. What is unclear is how the imitator ‘knows’ what motor activations will produce an action that look like the action produced by the model, especially given that the model and the imitator do not share the same embodiment and affordances. Many different accounts have been put forward to explain the correspondence problem, which fall into two main categories: specialist or generalist theories. Descriptions of the current theories of imitation are provided in **Table 2**.

1.3.1 Specialist theories of imitation

Specialist theories of imitation suggest that imitation is mediated by an innate ‘special purpose’ imitation mechanism. Meltzoff and Moore (1977) provided the first evidence for the active intermodal mapping (AIM) theory (as described in **Table 2** and **Figure 2a**) in demonstrating that within the first hour of life newborn infants spontaneously imitate manual and facial gestures, head movements and tongue-protrusion gestures. Furthermore, the authors demonstrated that infants imitated actions from memory sometime after the action had been observed (Meltzoff and Moore, 1989). Spontaneous imitation has also been observed in species closely related to humans such as newborn chimpanzees (Myowa, 1996) and in infant macaques (Ferrari et al., 2006); however, unlike humans, spontaneous imitative behaviours are only observed in the first months of life.

Another specialist theory is the direct-mapping theory (Butterworth, 1990) (described in **Table 2**) which proposes that the motor system of the imitator receives direct input from observing the actor’s movement. Perhaps the strongest evidence in favour of the direct-mapping approach comes from neurophysiological observations e.g. increased EMG activity recorded in the arm while observing arm-wrestling (Berger and Hadley, 1975). However it has been argued that the direct-mapping approach does not seem to fully capture the complexity of human imitative behaviour. For example, a direct-mapping approach would be counterproductive in situations involving joint action (where two or more people perform complimentary actions to achieve a shared goal). Similarly, the direct-mapping theory cannot easily account for the fact that 18-month-old infant are able to infer what an adult model intended to do when the model failed to perform an intended act (Meltzoff, 1995), and that children tend to emulate the goal of a model’s observed action as opposed to faithfully reproducing the model’s action (Bekkering et al., 2000). These findings indicate that children comprehend the similarity between observed acts and performed acts on a higher cognitive level (Wohlschläger et al., 2003).

Table 2: Theories of imitation.

Specialist theories of Imitation		**Generalist theories of Imitation**	
Direct-mapping theory	“An action is understood when its observation causes the motor system of the observer to 'resonate’.” (Rizzolatti et al., 2001). This ‘resonance’ of the motor system is believed to prime the motor system to produce the action being observed via the MNS.	**Ideomotor theory (IM)**	Associations are acquired between sensory and motor representations of actions, such that observing an action triggers a sensory representation of the action. This initiates the pre-activation of an internal motor representation due to similarity between the observed action and the motor representation (Prinz, 1997).
		Associative sequence learning theory (ASL)	Over time a bidirectional ‘vertical’ associative link is formed between sensory and motor representations, allowing imitation to occur when there is a matching vertical association between the sensory and motor representation (Heyes, 2005).
Active intermodal mapping theory (AIM)	Observation of an action triggers a visual representation of the action which is translated into a ‘supramodal’ representation encoding proprioceptive information in infant imitation, which forms the basis of adult imitation which later become coded in terms of action goals (Meltzoff and Moore, 1997).	**Goal-directed theory of imitation (GOADI)**	Observation of an action would undergo a decomposition-recomposition process, creating a hierarchy of goals, with priority being given to the end point of the action (goal) as opposed to the means by which the goal is achieved. This goal representation would activate the motor program most commonly associated with the goal (Bekkering et al., 2000; Wohlschläger et al., 2003).
		Dual-route theory (Rumiati and Tessari, 2002)	The direct route is used for the imitation of novel, meaningless actions. The indirect route is used for the imitation of familiar meaningful or goal directed actions (Rumiati and Tessari, 2002).
		Dual-route theory (Ferrari et al., 2009)	The direct route exerts a direct influence on motor output during action observation via the MNS. The indirect route connects the MNS to higher prefrontal cortical areas, allowing more complex cognitive and behavioural functions, such as integration of motivational or contextual factors (Ferrari et al., 2009).

1.3.2 Generalist theories of imitation

In contrast to specialist theories, generalist theories propose that imitation is dependent on experience and uses existing mechanisms. The ideomotor (IM) theory **(Figure 2b)**, described in **Table 2**, suggests that associations are acquired between sensory and motor representations of actions which share a common coding. It is mainly based on evidence from automatic imitation studies described in **section 1.2** (Brass et al., 2000, 2001a).

In the alternative ASL theoretical model, described in **Table 2**, action observation directly primes action execution via vertical associations between the sensory representation of an action and the motor representation of that action, which are thought to be formed during the course of development via general associative learning. Two types of vertical associations are described within this framework: direct vertical associations (without the need for intermediate action representations), or through indirect vertical associations which are mediated by another sensory representation, typically a word or phrase in humans (Heyes, 2001) **(Figure 2c)**.

A number of observations support the ASL theory. For instance, it was been shown that the accuracy of imitation and the range of behaviours imitated increase during an infant's development (Jones, 2009). Additionally, there is variation in development of imitative skills which is dependent on the quality of experiences and social interactions in which the adult and infant see and perform the same action (McEwen et al., 2007). Furthermore, the view that imitation is an innate ability has been more recently been challenged with the suggestion that tongue protrusion is the only behaviour that is reliably imitated by newborns. It has also been argued that tongue protrusion might be mediated by either an innate releasing mechanism or an oral exploratory response, as opposed to imitation (Anisfeld, 1996).

It has also been suggested that differences in imitation between chimpanzees and children could be due to motivation rather than ability (Heyes, 2005; Shea, 2009) since children are rewarded by adults from early infancy for performing previously observed actions (Pawlby, 1977). In line with this idea, studies have shown that children who were more frequently rewarded for imitating tended to imitate more (Waxler and Yarrow, 1975). This theory has also been addressed experimentally in 'counter-imitation' studies, which have demonstrated that it is possible to train a participant to form an associative link between an observed action and an incompatible action. Such incompatible training consequently led to the removal of the compatibility effect when observed and executed actions were compatible (Heyes et al., 2005).

The goal-directed theory of imitation (GOADI), described in **Table 2**, extends such generalist theories, claiming that imitation is coded based on the inferred goals of the model (Bekkering et al., 2000; Wohlschläger et al., 2003). GOADI is similar to the AIM model in that the processes mediating imitation involve the recoding of 'intermediate' action representations (rather than a direct link between sensory and motor representations). The strongest evidence in favour of this model of imitation comes from evidence that when instructed to imitate, children and adults tend to prioritize the reproduction of the overall 'goal' (i.e. the end point of the action), over the reproduction of the 'means' by which the goal is achieved, i.e. the choice of effector and movement trajectory (Bekkering et al., 2000).

There are also two further dual route models within the current literature on imitation (in addition to the ASL model, which also consists of two routes). According to Rumiati and Tessari's (2002) dual route model **(Table 2 and Figure 3a)**, the direct route is automatically selected to imitate meaningless actions, while the indirect route (using long-term semantic memory) is selected for imitation of meaningful actions. This proposal is based on the observation that imitation of meaningless actions was less accurate than meaningful actions when these action types were presented in separate blocks of trials, but no difference in accuracy was observed when these two types of action were presented within a mixed block of trials. Tessari and Rumiati (2004) proposed that while meaningless actions must be imitated using the 'direct' route, as the action would not be represented in long-term memory, the route for meaningful actions might be strategically selected. Thus, the indirect route may be selected for meaningful actions in the blocked condition, causing an advantage in accuracy. However, they suggest that the lack of an accuracy advantage in the mixed condition may be due to strategic selection of the direct route for both actions types, to avoid switching costs in the mixed condition, which may outweigh the advantage of the indirect route for meaningful actions.

Press and Heyes (2008) have since contested this hypothesis, proposing an alternative interpretation for Tessari and Rumiati's (2004) findings. They replicated the effect of the superiority of imitation of meaningful actions relative to meaningless actions in the blocked condition, but not in the mixed condition. However, when they examined imitation of meaningful and meaningless actions in the mixed condition as a function of the action type presented in the previous trial, this revealed that actions were imitated faster and more accurately when they followed a meaningful, rather than meaningless, action trial. They argued that if meaningful and meaningless actions are both imitated by the direct route, as suggested by Tessari and Rumiati (2004), they should place equal demands on working memory, and there should be no effect of the preceding action type on imitation of the present action. Therefore, they suggested that meaningless actions are imitated by the direct route which makes heavy demands on short term/working memory resources relative to processing of meaningful actions via the indirect route, consequently causing the detrimental effect on performance in the subsequent trial.

Ferrari and colleagues (2009) have also proposed a dual route model comprised of a 'direct' and 'indirect' route (described in **Figure 3b** and **Table 2)**. This model is based on the fact that imitation can be delayed in time with respect to the observed action, suggesting inhibitory control over imitation via the indirect route. It has been observed that patients with prefrontal lesions (Lhermitte et al., 1986; Brass et al., 2003) tend to uncontrollably imitate actions even when explicitly requested to inhibit imitation; supporting the idea the prefrontal cortex might play a role in the control of imitative behaviour.

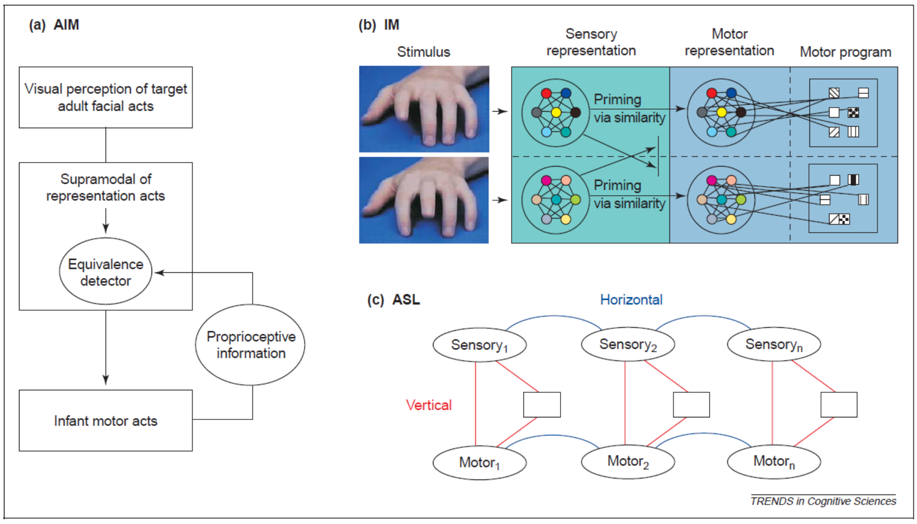

Figure 2: Three models proposed to explain the 'correspondence problem' of imitation as described in Table 2: **a)** AIM theory, **b)** IM theory; **c)** ASL theory (Brass and Heyes, 2005).

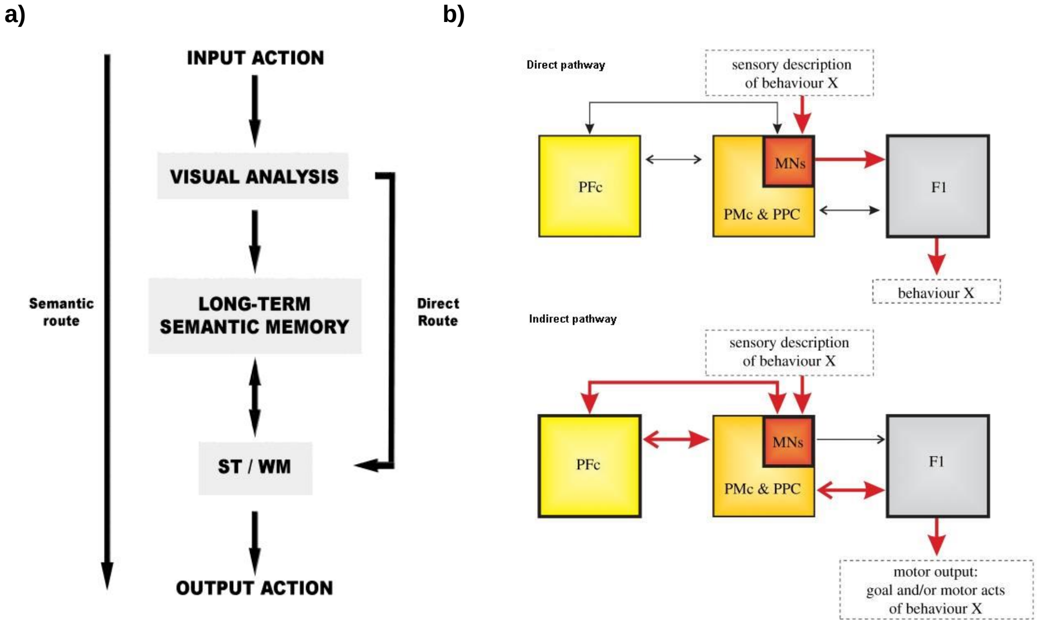

Figure 3: Dual route models: **a)** Rumiati and Tessari's (2002) dual-route model of imitation. ST/WM = short term/working (Tessari et al., 2007); **b)** Ferrari et al. (2009) dual route model: the direct mirror pathway (top) is shown by the red arrows. The black arrows show that the anatomical connections exist but are not fully functional; the indirect mirror pathway is shown below (Ferrari et al., 2009).

These theories of imitation incorporate both voluntary and involuntary imitation, being used by a number of authors to explain the RT advantage gained when observing a compatible movement (and RT disadvantage when observing an incompatible movement) observed in automatic imitation paradigms. Furthermore, the discovery of the MNS, which will be described in **section 1.4**, has provided a candidate neuronal mechanism for imitation.

1.4 Neural substrate for imitation: the mirror neuron system

The dominant neural explanation for imitation, including automatic imitation, is that the link between observed and executed actions is mediated by the MNS. Mirror neurons, which have been described by some as ‘the most important finding of the last decade in neuroscience’ (Ramachandran, 2000), have generated a great deal of interest and excitement, including considerable attention from the media (e.g. Jarrett, 2010). The MNS has consequently been researched intensively, leading to numerous new hypotheses regarding human behaviour, human evolution and neurodevelopmental disorders, such as ASC.

In a seminal paper published in 1992, di Pellegrino and colleagues described a series of electrophysiological experiments providing evidence for the existence of a subset of neurons with both visual and motor properties within a subdivision of the premotor cortex (area F5) of the macaque monkey. They observed that a subset of neurons in area F5 discharged not only in response to performance of a motor action (such as grasping food), but also in response to observation of the experimenter performing that same motor action (i.e. observing the experimenter grasping food) (di Pellegrino et al., 1992). The fact that the observation of an action activated the same neurons in the brain of the observer that are normally activated when performing the action, implies that observer’s motor system represented the observed action as if the observer were performing the action. Thus these neurons ‘mirrored’ the neural activity of the actor. On this basis, these neurons were termed ‘mirror neurons’. Soon after their discovery it was proposed that the properties of MNs could allow ‘direct-matching’ of observed and executed actions, providing a straightforward solution to the correspondence problem of imitation (Iacoboni et al., 1999).

On the basis of single-cell recording evidence, the presence of MNs in the monkey brain is widely accepted. The neurons within area F5 have been categorized into two classes: canonical neurons; which respond to the mere observation of a graspable object and during the performance of a motor action, and MNs; which respond during the performance of a specific motor action as well as when observing another individual performing that same specific motor action (Rizzolatti et al., 1996). Gallese and colleagues (1996) also observed that there was a clear relationship between the visual action particular MNs responded to, and the motor response that they coded. On this basis, MNs have been further subdivided into two categories: 1) strictly congruent MNs, which respond only to the observations of same action which is coded for by a particular neuron, and 2) broadly congruent MNs, which fire for related actions (di Pellegrino et al., 1992) or different actions that achieve the same goal (Gallese et al., 1996). Approximately one third of MNs are strictly congruent and may play a role in imitation and mimicry. The remaining two thirds are broadly congruent MNs, which may play a role in emulation and in social interactions in which individuals perform complimentary actions to achieve a shared goal (Gallese et al., 1996). In monkeys, MNs respond to goal-directed actions, which refers to actions in which an effector (i.e. hands or mouth) interacts with an object; for example grasping, holding, biting, tearing or breaking an object. A subclass of MNs, known as audiovisual MNs, was observed to also respond to sounds related to an action (e.g. the sound of a peanut breaking) (Kohler et al., 2002). In addition to the IFG, further studies reported the presence of MNs in the inferior parietal lobule (IPL) (Fogassi et al., 2005).

Neuroimaging studies using positron emission tomography (PET) (Rizzolatti et al., 1996) and functional magnetic resonance imaging (fMRI) (Iacoboni et al., 1999) provided the first evidence of a MNS in humans, revealing a likely homologue of area F5 of the macaque brain. They observed activity consistent with that seen in macaque brain area F5, in the human inferior frontal gyrus (IFG) as well as the inferior parietal lobule (IPL) **(Figure 4a)**. Together, the IFG and IPL represent the human MNS. The main visual input to the MNS originates from the superior temporal sulcus (STS), an area which is known to code biological motion (Perrett et al., 1989) **(Figure 4b)**. Studies have since shown a clear anatomical homology between the IFG in humans and area F5 of the macaque brain (Petrides and Pandya, 1994).

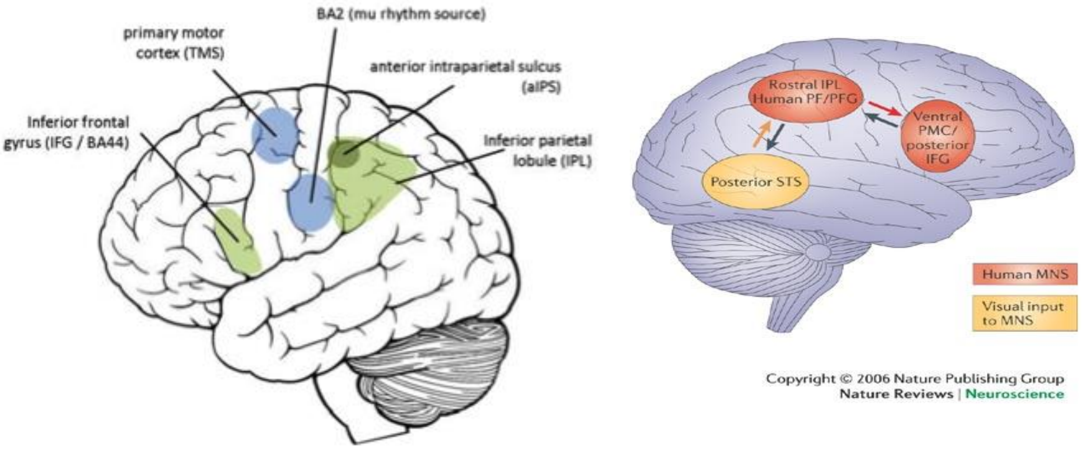

Figure 4: The human MNS: **a)** MNs exist in the human inferior frontal gyrus (IFG; Brodmann'sarea 44/Broca's area and the inferior parietal lobule (IPL; Brodmann's area 40) (indicated in light green). BA2 – the somatosensory cortex (indicated in blue) is the source of the mu rhythm. TMS measures are sensitive to the excitability of the primary motor cortex (indicated in blue) (Hamilton, 2012); **b)** The IPL, IFG (and STS) make up the human MNS (and its associated brain areas) (Iacoboni and Dapretto, 2006).

fMRI relies on the fact that cerebral blood flow and neuronal activation are coupled; thus brain activity can be measured by detecting changes in blood flow known as the blood oxygen dependent level (BOLD) signal. fMRI adaptation (or repetition suppression) is a technique which relies on the fact that the magnitude of the BOLD signal consistently deceases or 'adapts' on repeated presentation of a stimulus relative to presentation of a novel stimulus. Using an fMRI adaption paradigm, Kilner and colleagues (2009) demonstrated that responses were suppressed in the human IFG both when an executed action was followed by the same rather than a different observed action, and when an observed action was followed by the same, rather than a different executed action. Since this pattern of activity could only be mediated by a neuronal population that responds to both action observation and action execution, this study provides evidence in favour of the existence of a human MNS in the IFG.

Further evidence has been provided by studies using single pulse transcranial magnetic stimulation (TMS). Stimulating the primary motor cortex with TMS **(Figure 4a)** induces a current in the underlying neural tissue, triggering action potentials in neuronal axons, which subsequently produce a peripheral muscle twitch termed a motor-evoked potential (MEP). MEPs can be recorded from the peripheral muscles using EMG allowing one to measure sub-threshold motor excitability due to the fact MEP amplitude is positively correlated with motor excitability. Using TMS, Fadiga et al. (1995) observed that the pattern of muscle activation during observation of the action corresponded to the pattern of muscle contraction present when performing the same action. This observation has been corroborated by a number of research groups (Hari et al., 1998; Strafella and Paus, 2000; Gangitano et al., 2001). The observation that during the passive observation of actions, MEP facilitation occurs specifically in the same muscles that would be used to perform the observed action seems particularly relevant with regard to neural mechanisms of automatic imitation.

In addition, electroencephalography (EEG) studies from as early as 1954 have found neural activity in the somatosensory cortex when subjects observed others performing motor actions. Gastaut and Bert (1954) observed an electromagnetic wave oscillating at 8-10Hz over the somatosensory cortex (Brodmann's area 2; BA2) known as the mu rhythm **(Figure 4a)**. They found that the mu rhythm was strongly suppressed not only during motor activity but also when observing actions performed by others. Several studies using electroencephalography (EEG) or magnetoencephalography (MEG) have corroborated this finding, reporting an attenuation of cortical oscillatory activity during movement observation that is similar to activity observed during movement execution (Cochin et al., 1998; Babiloni et al., 2002; Hari et al., 2000). Since the discovery of MNs it has been hypothesized that mu rhythms may reflect the downstream modulation of MNs. Mu rythms have therefore been used as a biological marker of MNS activity (Muthukumaraswamy et al., 2004).

Most convincingly, Mukamel and colleagues (2010) provided the first evidence that MNs exist in the human frontal lobe at a neural level. The extracellular neural activity of 21 human patients has been directly recorded during execution and observation of emotional facial expressions and grasping actions. In line with previous findings, they observed a certain population of neurons in the medial frontal lobe that responded to both observation and execution of action.

Naturally there has been a great deal of debate and speculation concerning the potential function of the MNS. Numerous speculative theories have been proposed which suggest that the MNS may play a role in a range of complex cognitive processes, such as action intention understanding (thought to be a precursor to 'theory of mind' (ToM) - the ability to attribute mental states to others), sensorimotor learning, language development (Arbib, 2002) and empathy (Wicker et al., 2003; Carr et al., 2003; Leslie et al., 2004); however, there is currently not enough conclusive data to fully support these theories.

However, given that the MNS maps motor actions of observed actions, it constitutes an ideal mechanism to explain imitation. Furthermore, there is significant evidence to support the proposed link between the MNS and imitation. For example, using fMRI Iacoboni and colleagues (1999) measured the brain activity of healthy human participants in three conditions; during observation-only, performance-only and during imitation (both observation and execution) of video clips of a moving finger. They postulated that 1) some brain regions should be active during finger movement in all of these conditions, and 2) that since during imitation one simultaneously observes and performs an action, the highest activity would be observed during imitation, compared to observation or performance alone. They found two brain regions which possessed both of these properties: the IFG and the IPL, thus supporting the idea that imitation is mediated by the MNS.

Similar results were obtained in further fMRI studies which showed the same progressive sequence of brain activations in MNS regions during both observation and imitation of grasping actions (Nishitani and Hari, 2000), grasping pantomimes (Grèzes et al., 2004), and verbal and non-verbal lip forms (Nishitani and Hari, 2002). In addition, an fMRI study has indicated that the IFG may also be utilised in imitative learning. Patterns of brain activity representing the MNS in musically naïve participants were sequentially activated during both observation of guitar chords played by a guitarist, and self-execution of observed chords (Buccino et al., 2004). Furthermore, it has been observed that induced 'virtual lesions' of the right and left IFG using low frequency repetitive rTMS (which has been shown to induce sustained reductions in activity in the part of the brain that has been stimulated) causes significant impairment to the imitation of finger movements (Heiser et al., 2003). This suggests an important role for IFG in imitation. Taken together, these studies support the idea that the MNS could provide a mechanism to explain some forms of human imitation, including imitative learning.

The main argument against a role for MNs in imitation is that recognising an action being performed does not automatically lead to replication of that model's action. While the studies discussed suggest that the MNS might subserve the generation of imitative behaviour, it remains unclear whether or not imitation is the function for which MNs evolved. Specialist theories would suggest that this is the case; however generalist theories imply that although MNs are capable of generating imitative behaviour imitation is not their innate function, and imitative properties are acquired through associative learning. The question of whether the properties of MNs are innate or acquired during development is still under debate. Interestingly, studies have shown that MN activity can be altered in response to observational learning. For example, it was initially observed that macaque MNs only fired when the monkey observed an experimenter grasping food with their hand, but not when using pliers to grasp the food (Gallese et al., 1996). However, in a later study, a population of MNs, conversely, discharged more in response to performance of actions using tools than actions performed with hands (Ferrari et al., 2005). Since monkeys are not naturally familiar with the use of human tools, it is plausible that the change in MNS response occurred through visual experience of repeatedly observing humans using tools in the laboratory setting, providing evidence that the MNS can be altered through observational learning.

Furthermore, if automatic imitation/motor mimicry is mediated by the MNS (Blakemore and Frith, 2005), the magnitude of automatic imitation effects can theoretically be used to measure MNS function. If, as is commonly assumed, automatic imitation represents the same phenomenon as motor mimicry, a greater understanding of the processes mediating automatic imitation could further our understanding of the control of motor mimicry.

It has also been proposed that perhaps only automatic imitation, and not voluntary imitation, is mediated by direct matching of the MNS (Byrne, 2005). This theory stems from the puzzling question as to why monkeys, who have a MNS, do not acquire novel skills and behaviours by imitation (Visalberghi and Fragaszy, 1990). Byrne (2005) proposes that since monkeys have been shown to recognize when they are being imitated (Paukner et al., 2005), but seem unable to learn by imitation, perhaps imitation can be seen as two different capacities: 1) social mirroring, when actions are matched and have social benefits; and 2) learning by copying, when new behavioural routines are acquired by observation. In contrast, the ASL model of imitation argues that both voluntary and involuntary imitation are mediated by the same psychological processes (Heyes, 2005).

1.5 Factors influencing automatic imitation

It is generally acknowledged that the perceiver’s past experience, intentions, expectations, and attention influence visual perception. The effects of previously stored information on the processing of a stimulus are known as ‘top-down’ effects, due to the fact they are thought to originate from higher cognitive processes at a high level within the hierarchy of visual processing, exerting their influence at lower levels in order to influence our perception (Carlson, 2010). In contrast, ‘bottom-up’ processing refers to the processing of a stimulus based solely and directly on the visual information arriving from the retina to the visual cortex, which forms our perception of the stimulus without the influence of higher cognitive processes. It is referred to as ‘bottom-up’ since sensory input is considered a low level in the visual processing hierarchy, and this information is then processed by successively higher levels of the visual processing hierarchy until the highest levels (the ‘top’ of the system) is reached, and the object is perceived (Carlson, 2010).

Much of the evidence for the role of both bottom-up and top-down factors in automatic imitation comes from agency studies, which have compared the magnitude of automatic imitation effects generated by biological (i.e. human) and non-biological (i.e.

robotic/object) stimuli. Comparing automatic imitation effects between human and non-human stimuli is of interest because if as is generally assumed, automatic imitation effects are based on MN activation, according to specialist theories of imitation one would expect the behavioural advantage to be specific, or at least maximally responsive, to human actions. In line with this, it has been consistently found that observed human movements produce stronger automatic imitation effects relative to non-human movements (Brass et al., 2001a; Gowen et al., 2010; Kilner et al., 2003) supporting the theory that the brain processes these types of movement differently.

Biological motion processing occurs rapidly and efficiently in adult humans, and it has been suggested that specialised neural mechanisms exist for this purpose within the STS (Grossman et al., 2000). It is known that the STS receives input from form and motion areas, and thus it is a likely location for the integration of form and motion processing (Vaina et al., 2001). The term biological motion refers to the characteristic, non-rigid patterns of movement produced by humans and animals (within the biomechanical constraints of their skeletal structure). From the time of birth, infants are known to prefer to look at biological motion over scrambled/inverted patterns (Simion et al., 2008), indicating an innate preference for biological motion. Biological motion has typically been studied using point-light displays, in which point-lights are placed on the joints of the body of an actor who is otherwise rendered invisible in the dark. From minimal information provided by point-light displays, adult observers are able to easily identify types of actions, recognise familiar people (Troje et al., 2005) and even read subtle details such as the age, gender, intentions and emotional state of the actor (Barclay et al., 1978; Blakemore and Decety, 2001; Dittrich et al., 1996; Mather and Murdoch, 1994; Troje, 2002). These findings demonstrate that human adults are highly attuned to the perception of biological motion.

Neuroimaging studies have shown that similar activity is induced in the STS for ‘real’ biological motion as for simplified displays of biological motion (such as point light walkers) (Grossman et al., 2000; Grèzes et al., 2001). However, scrambled point light displays (Stanley et al., 2010), and non-biological motion (Cross et al., 2009) fail to activate the STS. One exception to this is that non-biological stimuli have been shown to induce activity in the STS when the inanimate object was attributed a mental state, as if it were animate (Castelli et al., 2000). Gallese and Goldman (1998) suggest that the capacity of the MNS to match observed with executed actions evolved to support higher socio-cognitive functions, such as understanding the mental states of others. If this hypothesis is correct we would expect a human bias of imitation since the MNS should not be tuned to movements of objects lacking mental states.

Alternatively, due to the fact that humans are a privileged class of stimuli, with a preference for attending to faces over non-social stimuli being present from birth (Fantz, 1963; Johnson et al., 1991), it could be argued that a human bias of automatic imitation has been observed due to the fact that humans tend to be socially motivated, thus finding interactions with human stimuli more intrinsically rewarding than with non-human stimuli. For this reason greater automatic imitation effects may be produced for human stimuli may be due to greater experience observing and executing human actions relative to non-human actions. The idea that the activity of the MNS is experience-dependant is consistent with findings from a number of studies (Engel et al., 2008; Cross et al., 2009; Calvo-Merino et al., 2006) and fits in well with generalist models of imitation (e.g. the ASL model).

However, although stronger automatic effects have generally been documented for human generated movements, the specificity of the MNS to human movement remains controversial. Inconsistencies in the literature exist, which suggest that when the visual saliency of the non-human stimulus is matched the magnitude of automatic imitation effects is similar for both human and non-human stimuli. In line with this, neuroimaging investigations comparing neural responses to biological and non-biological stimuli have also produced conflicting results. Some data indicates that the human MNS is biologically tuned and is not activated by non-biological movements (Heiser et al., 2003; Tai et al., 2004), while other studies have found little to no difference in activation of the MNS for biological versus non-biological movement (Gazzola et al., 2007; Jonas et al., 2007). It is possible that the mixed results regarding the degree of difference in imitation for biological vs. non-biological stimuli in different studies can be accounted for by an interplay between bottom-up and top-down factors influencing imitation (Gowen and Poliakoff, 2012). Multiple lines of evidence suggest that both bottom-up and top-down factors modulate imitative compatibility, and this evidence will be reviewed in **section 1.6 and 1.7**.

1.6 Bottom-up modulation

1.6.1 Lateral spatial compatibility

It has been argued that there are two possible sources of the influence of action observation on brain areas involved in action execution. The first possibility is that these effects represent a matching or ‘mirroring’ of motor representations during action observation, which primes action execution (automatic imitation). The second possibility is that the observed actions have up-down, left-right spatial properties, which could activate motor representations corresponding to these spatial properties, causing faster responses when the observed stimulus is spatially aligned with the location of the participant’s response, known as spatial ‘stimulus response compatibility’ (SRC) effects (Cho and Proctor, 2003). A similar but smaller advantage occurs in tasks in which a non-spatial stimulus attribute (e.g. colour) is relevant and stimulus location is irrelevant, known as the ‘Simon effect’. The Simon effect refers to the finding that RTs are usually faster and more accurate when the stimulus occurs in the same relative location as the response, even if the stimulus location is irrelevant to the task i.e. participants are faster to respond with their right hand to a stimulus appearing on the right and faster to respond with their left hand to a stimulus appearing on the left (Simon and Proctor, 1990).

In fact, in the majority of early studies of ‘automatic imitation’, the influence of spatial variables on action observation have not been fully investigated or controlled for. For example, in finger imitation studies where the responding finger matched the stimulus finger, not only in terms of the observed movement, but also in terms of spatial correspondence, imitative compatibility effects have potentially been confounded with spatial compatibility effects. For example, as shown in **Figure 5**, when required to respond using one’s right hand, an observed stimulus hand presented in a ‘mirror’ view would appear to be a left hand, thus appearing to be a mirror image of the participant’s responding right hand. In the mirror view, the participant’s own finger movement is in a laterally compatible spatial alignment with the observed finger movement (i.e. the observed movement occurs on the same side of the computer screen relative to the participant’s own finger movement). This is termed lateral spatial compatibility.

Due to the issue of lateral spatial compatibility occurring when a hand stimulus is presented as a mirror image of the participant’s hand, thus sharing the same spatial characteristics, a number of studies have attempted to control for spatial compatibility effects by using an ‘anatomical’ stimulus (Brass et al., 2000, 2001; Gowen et al., 2010; Jiménez et al., 2012). As seen in **Figure 5,** when required to respond using one’s right hand, an observed stimulus hand presented in an ‘anatomical’ view would appear as if an actor were facing the participant, using the hand which is anatomically compatible with the participant’s responding hand. In the anatomical view, the participant’s own finger movement is in a laterally incompatible spatial alignment with the observed finger movement (i.e. the observed movement occurs on the opposite side of the computer screen relative to the participant’s own finger movement). Lateral spatial compatibility is therefore effectively removed when stimuli are presented in the anatomical view.

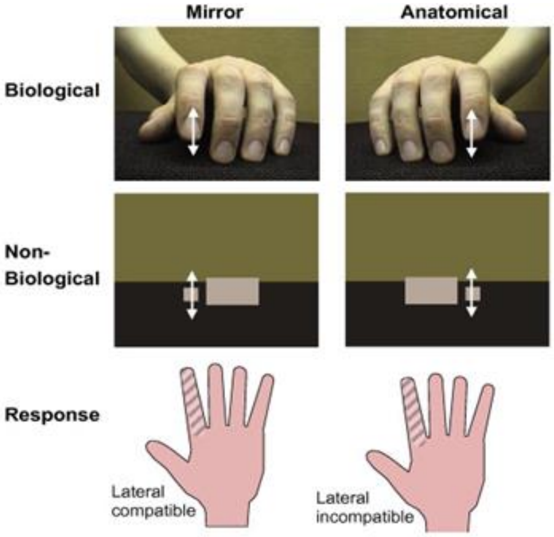

Figure 5: Mirror and anatomical representations of biological (hand) and non-biological (object) stimuli (Gowen et al., 2010).

A number of different groups have attempted to demonstrate that imitative compatibility is not reducible to SRC effects as some researchers have argued (Jansson et al., 2007). Using a variety of methods to separate confounding spatial SRC from imitative compatibility effects, a large body of evidence supports the existence of a separate imitative compatibility component which is not reliant on compatible spatial codes. This evidence strongly supports the idea that imitative and spatial compatibility effects are in fact mediated by separate cognitive processes. These studies will be described in further detail in **section 3.1**. Importantly, these findings emphasize that it is crucial to account for the potential confound of spatial SRC effects in automatic imitation paradigms, an issue which has been addressed throughout the current thesis.

1.6.2 Visual saliency and kinematics

A variety of different go signals have been used in different paradigms, which include the movement itself, a separate visual go signal, or an auditory go signal. Studies have shown that visual saliency of the go signal can influence automatic imitation effects. For example, Brass et al. (2000) compared using a symbolic go signal (a number) with using the finger movement itself as the go signal. They found that participants reacted faster when the finger movement itself provided the go signal, as opposed to the number go signal **(Figure 6a**). In their second experiment, Brass and colleagues replaced the number go signal with a spatial go signal (an X on the fingernail of the index finger or the middle finger) **(Figure 6a)**, and found that again RTs were faster for a finger movement compared to a spatial go signal. Brass et al. (2000) suggested that imitating a movement is easier than imitating an abstract go signal. These findings indicate a human finger movement may be much more salient as a go signal than the appearance of spatial or symbolic go signals. This may be in part due to the fact the finger itself is much larger and brighter than the cross or numbers. In addition, as previously discussed **(section 1.5)** biological movement itself is highly salient.

Similarly, Gowen et al. (2010, Experiment 1) used the onset of a cross (X) rather than the onset of movement as a go signal **(Figure 8a)**. This change led to a reduction in compatibility effects compared to previous studies (Brass et al., 2001a), suggesting that the greater saliency of biological movement as a go signal may be responsible for stronger automatic imitation effects in previous studies. This issue was also directly explored by Aicken et al. (2007), who found that when the size of the go signal (an X) was increased, participants' RTs were faster relative to a smaller, less salient x **(Figure 6b)**.

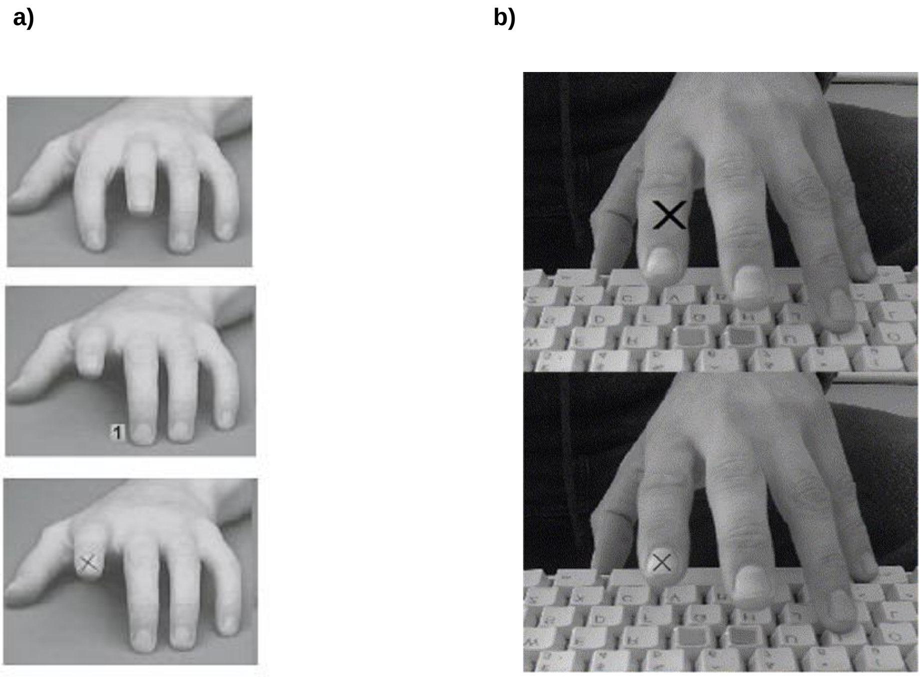

Figure 6: a) Participants RTs were faster in response to the finger movement condition (top) compared to the symbolic (number) go signal (middle) or spatial (x) go signal (bottom) (Brass et al., 2000); **b)** Increasing the visual salience of the cross go signal caused faster RTs (Aicken et al., 2007).

Evidence from several studies indicates that manipulating the surface characteristics of a stimulus can directly affect the strength of automatic imitation effects produced. For example, Press et al. (2005) directly investigated whether automatic imitation is sensitive to the human-like appearance of the stimulus. In their first experiment, they created a robotic stimulus by simply adding a metal and wire ‘wrist’ to a real human hand. They instructed participants that the hand was robotic; however automatic imitation effects were similar for the real versus ‘robotic’ hand. In their second experiment, they used a genuine robotic hand **(Figure 7a)**, and found that stronger imitative compatibility effects were generated for the human hand relative to the robotic hand. Based on these findings, they concluded that bottom-up factors (i.e. the surface characteristics of the stimuli), and not top-down processing of human stimuli is responsible for modulating the strength of automatic imitation effects.

In contrast, Jansson et al. (2007) found no difference between automatic imitation effects generated by pen and dot stimulus movements **(Figure 7b)** compared to finger and hand movements respectively. Based on these findings, Jansson and colleagues (2007) argued that automatic imitation may be due to simple stimulus response characteristics (i.e. spatial or ‘conceptual’ compatibility effects), and thus previous findings of a human bias may have resulted from unmatched visual stimulus saliency between biological and non-biological stimuli.

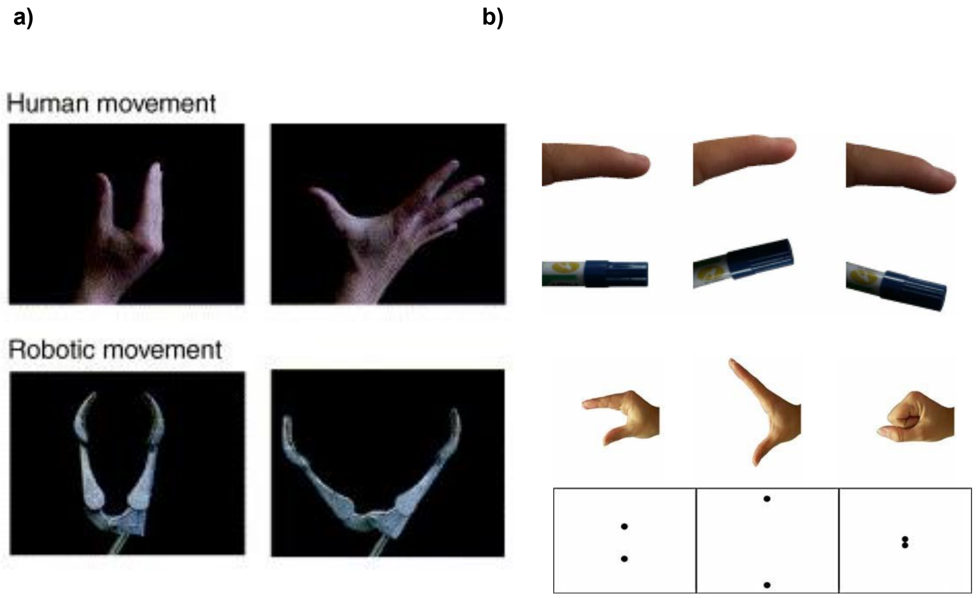

Figure 7: a) Automatic imitation paradigm using human and robotic hand movements (Press et al., 2000); **b**) Biological stimuli and non-biological stimuli used by Jansson et al. (2007).

In line with Press and colleagues (2005) findings, Kilner et al. (2003) demonstrated that while observing a human perform incongruent arm actions had a significant interference effect on executed actions, no interference effects were produced when observing a robotic arm make incongruent movements. In contrast, Oztop et al. (2004) found that interference effects were produced when participants observed a humanoid robot, which had a more human-like appearance. Since the movement kinematics of the robotic stimuli used by both Kilner et al. (2003) and Oztop et al. (2004) followed a biological profile, the discrepancy in results suggests that shape and surface characteristics of the stimuli has an effect on automatic imitation, such that if the stimulus looks more human-like it is processed differently.

In addition to physical differences, the kinematics profiles of human and non-human movements differ. Biological movements are non-linear and more variable than non-biological movements, following a bell-shaped velocity profile: starting slowly, accelerating to the mid-point and decelerating towards the end of the movement, in contrast to the constant velocity profile of non-biological movements (Hogan, 1984). Some groups have examined whether biological versus non-biological kinematics modulate the magnitude of automatic imitation effects. For example, Kilner et al. (2007) found that altering the velocity profile of a biological stimulus to make it appear non-biological (while keeping surface characteristics constant) removed the previously observed interference effect. These findings indicate that biological kinematics play a role in the emergence of automatic imitation effects, regardless of surface shape characteristics.

Importantly, these findings indicate that stimulus saliency is a potential confound in automatic imitation paradigms. It has been noted that the majority of studies comparing automatic imitation effects between biological and non-biological stimuli have not controlled for stimulus saliency. This is surprising given that human and robotic stimuli generally differ on a number of dimensions, including shape, kinematics, size, colour and luminance.

Typically non-biological stimuli tend to be smaller, coving less surface area and have a lower luminance than biological stimuli (Gowen and Poliakoff, 2012) and thus may be less visually salient than biological stimuli. Therefore studies which have used biological and non-biological movement as the go signal and have not controlled for factors such as size, shape, luminance, might not provide evidence for the enhanced processing of biological stimulus driven by the MNS, but rather reflect unmatched stimulus saliency. In the current thesis, the issue of the visual saliency of the go signal is addressed by using a separate yellow flash go signal, for both stimuli as opposed to the movement itself. Size and luminance between the biological and non-biological stimuli has also been controlled for (see **Appendix C1**).

While the outlined studies clearly imply that bottom-up characteristics of stimuli influence the strength of automatic imitation, the literature is by no mean consistent. For instance, it is unclear why Press et al. (2005) found stronger automatic imitation for a human compared to robotic hand, whereas Jansson et al. (2007) found equivalent imitation effect for a hand and two dots. In addition, the fact that Press et al., (2007) found that compatible training with a robot hand led to similar levels of imitation as a human hand appears to argue against a consistent role for stimulus saliency, since imitation increased while stimulus saliency remained the same. Importantly, emerging evidence suggests that a role for top-down factors in automatic imitation might explain the inconsistencies in the levels of automatic imitation for biological and non-biological stimuli measured in the described literature.

1.7 Top-down modulation

Social ‘motor mimicry’ of observed behaviours is not a ‘default’ behaviour in healthy adults; it is clearly modulated by a number of factors, including the goals and intentions of the individual and the situational context. For example, under normal circumstances seeing another individual smiling may cause involuntary mimicry of that behaviour. However, healthy adults are normally able to suppress the impulse to smile if mimicry is inappropriate e.g. if one has knowledge of deceptive intentions behind their smile.

Mimicry has been shown to be modulated by social contextual factors such as friendship, desire to affiliate and social status. For example, people imitate people they like more, or who are members of the same religious/ethnic group compared to people they dislike or who are members of a different religious/ethnic group (Heider and Skowronski, 2008; Yabar et al., 2006; Likowski et al., 2008; Stel et al., 2010). People also tend to imitate more when they are feeling socially excluded (Lakin et al., 2008). These findings imply that even though mimicry occurs unconsciously, it is not entirely unselective and unsophisticated imitation, but rather is under subtle control by a number of modulating factors.

In addition, there are clearly control mechanisms for the inhibition of imitative tendencies, as to be constantly and uncontrollably imitating observed actions would be maladaptive in everyday life. A mechanism to suppress inappropriate mimicry would therefore be equally important for harmonious social interactions to take place. Surprisingly, very few studies to date have investigated the potential existence of a neural mechanism for the inhibition of our natural tendency to imitate.

Higher prefrontal regions of the brain have been implicated in inhibition of imitative compatibility. The prefrontal cortex is a neural region known to be involved in more complex cognitive processing and executive functions (Stuss and Benson, 1984). Neuropsychological support for the existence of an inhibitory mechanism of imitative compatibility comes from evidence that frontal lobe damage is associated with a condition called echopraxia, in which a person involuntarily imitates the actions of another person. It was initially observed by Luria in 1966 that patients with frontal lobe damage displayed unwanted imitation of observed movements. This finding was later replicated by Lhermitte and colleagues (1986) who found patients with frontal lobe damage were unable to inhibit imitative response tendencies even when explicitly asked not to imitate.

Bearing in mind that automatic imitation it believed to represent a tightly controlled experimental form of naturalistic motor mimicry; automatic imitation is also likely to require a mechanism for inhibiting imitation. In line with the idea that the frontal neural areas are involved in the inhibition of automatic imitation, Brass et al. (2003) used an effector compatibility paradigm to investigate whether inhibition of imitative behaviours was impaired in patients with frontal lobe lesions. Their results indicated that there was a stronger tendency to exhibit spontaneous imitative behaviour and a deficit in inhibition of imitation in patients with frontal lobe lesions, in comparison with patients with non-frontal lesions. These findings imply that our tendency to imitate is usually kept under control by suppression of unwanted automatic response tendencies via inhibition from the frontal lobe. In line with this idea, Brass et al. (2009) contend that if the mere observation of an action automatically activates its motor representation, then it is likely that a default inhibitory mechanism exists which avoids the overt reproduction of all observed actions.

Accumulating evidence suggests that higher cognitive processes interfere with the control and execution of automatic imitation. If automatic imitation is modulated by such higher cognitive processes, it raises questions as to what extent automatic imitation is in fact an ‘automatic’ process, as its commonly used name suggests. Based on the three criteria suggested by Posner and Snyder (1975), an automatic process must 1) occur unintentionally, 2) occur without conscious awareness, and 3) operate without interfering with other processes that demand limited attentional resources. It is clear that automatic imitation is automatic in the sense that it is independent of the one’s intentions and conscious awareness, since one is not instructed or required to attend to the task-irrelevant action, and a number of studies have shown that automatic imitation occurs when the task-relevant and task irrelevant stimuli are spatially separate (Leighton and Heyes, 2010). In addition, the fact that imitative compatibility effects occur due to interference from observing incompatible actions supports the idea that automatic imitation is independent of one’s intentions, since it is unlikely that one would intentionally interfere with one's own performance. However, emerging evidence suggests that the magnitude of imitative compatibility effects is strongly influenced by top-down factors such as social priming, (Cook and Bird, 2011) attention (Bach et al., 2007) and belief (Liepelt et al., 2008); as will be discussed in further detail in the following sections. These findings indicate that top-down processing plays an important role in the modulation of automatic imitation, thus automatic imitation cannot be considered 'automatic' in the sense that it is independent of interference from other processes.

1.7.1. Social priming

Recent studies have found that the magnitude of automatic imitation effects is modulated by social attitudes. Leighton et al. (2010) used a movement compatibility automatic imitation paradigm, in which participants opened their hand in response to the opening or closing of a human hand. They observed that participants who were subliminally primed (using a scrambled word priming task prior to the imitation task) with words promoting a pro-social attitude (i.e. friend, co-operate, together) showed a significantly greater imitative compatibility effect than participants who had been primed with words promoting an antisocial attitude (i.e. rebel, individual, disagreeable).

This social priming effect has been replicated by Cook and Bird (2011) who similarly primed participants with either pro-social or anti-social words prior to completing a finger movement effector compatibility automatic imitation task. Interestingly, they found that when participants were primed with neutral words, participants showed an imitative compatibility effect that was smaller than that of the pro-social priming group but larger than the anti-social group. Based on this finding they argued that it is plausible that pro-social attitudes decrease (and antisocial attitudes increase) inhibition of automatic imitation, relative to a baseline level of inhibition. It has been proposed that modulation of imitation (and by extension mimicry) by social attitudes may be part of a positive feedback loop in which pro-social attitudes generate imitation, and imitation and/or being imitated increases positive social attitudes (Leighton et al., 2010). Furthermore, they have speculated that a bidirectional relationship between naturalistic mimicry and pro-social attitudes could either be due to an innate tendency to imitate more when in an affiliative frame of mind, or as a result of learning through social interactions that it is in circumstances when the interacting partner is displaying a pro-social attitude that imitation tends to be most rewarding.

Further research will be required to understand the neural mechanism by which automatic imitation is modulated by social attitudes. It has been argued that susceptibility and resistance to imitative compatibility relies on inhibitory mechanisms that allow for the appropriate distinction between 'self' and 'other' (Brass et al., 2005). Therefore, it is possible that pro-social priming blurs the line between self and other, thus facilitating imitative compatibility effects. Conversely, anti-social priming may increase self-awareness, thus reducing or inhibiting imitative compatibility. This argument is supported by the fact that imitation is inhibited by self-focus induced by self-observation in a mirror or self-referential statements (Spengler et al., 2010).

The ASL model Brass and Heyes (2005) proposes that visual attention to an observed movement creates a sensory representation of the movement, resulting in the activation of a motor representation of that movement, which consequently creates the impulse to perform the movement. However, according to this account, this sequence of events only occurs provided that sensory and motor representations have become linked through previous experience observing and executing the movement. Based on this theory, two possible mechanisms have been proposed to explain modulation of imitative responses by social attitudes: 1) an attentional route may affect the probability that sensory representations of actions are activated, or 2) inhibitory mechanisms may suppress the probability that motor representations are activated by sensory representations, inhibiting overt mimicry. Leighton et al. (2010) argue that an inhibitory mechanism to explain social modulation of imitation is more plausible than an attentional route, as many of the imitation tasks used in such studies require participants to attend to the same part of the screen as the movement stimulus. In addition, an emerging pattern of data suggests that the effect of social priming was only evident in slower responses, supporting the hypothesis that social modulation of mimicry is likely to be caused by the late process of inhibition, rather than an attentional process (where effects would also be expected to be present for faster responses).

1.7.2 Attention

A number of studies have provided convincing evidence that the strength of automatic imitation is influenced by intentionally mediated changes in spatial attention. For example, Bach et al. (2007) demonstrated that spatial attention must be oriented to the action-related effector in order for imitative compatibility effects to be produced. The participants observed hand or foot actions and were required to press a foot key if an overlaid target was of one colour, and a finger key if the target was of the other colour. Thus, the responses of the participants were either similar or dissimilar to the presented irrelevant action. However, they found when the target drew attention away from the action-related effector (hand or foot) to another body part (head) the automatic imitation effect was absent.

Similarly, Chong et al. (2009) corroborated findings of a strong influence of attention in automatic imitation. Using a go/no-go paradigm, in which participants were required to perform either a precision or power grip, they replicated previous findings of automatic imitation when participants were required to use grip as a go signal. However, they found that they were required to use the colour of a spatially distinct but overlapping stimulus as the go signal, automatic imitation did not occur. They also found that when participants were required to attend to the laterality of the stimulus hand, the automatic imitation effect disappeared. These findings indicate that automatic imitation was contingent on attention being directed to a feature of the observed hand that was relevant to their responses.

Another study, the results of which form the basis for the hypotheses of experiments 1a and 1b of the presented work, has recently highlighted the importance of attention in modulating automatic imitation effects (Gowen et al., 2010, Experiment 2b). They used a simple automatic imitation paradigm in which participants executed a pre-specified finger movement while viewing compatible and incompatible finger and object movements **(Figure 8)**. In Experiment 1 they used a cross which appeared on the stimulus as the go signal **(Figure 8a)** automatic imitation was produced for the finger movements only; however they found increased automatic imitation effects in the mirror view, indicating a strong influence of spatial SRC. In order to reduce lateral spatial compatibility, which may have been increased due to the use of a cross go signal appearing on the moving stimulus, they used a more spatially neutral go signal - a yellow flash **(Figure 8b)-** in their second experiment. In Experiment 2, ‘oddball’ trials consisting of a small ‘stutter’ during stimulus movement were also included. Half the participants were required to verbally report oddball trials (instructed group), while the other half of the participants were not informed about the oddball trials (no-instruction group). The aim of the oddball manipulation was to draw attention towards the movement of biological and non-biological stimuli. They hypothesized that consistent with their first experiment, stronger imitative compatibility effects observed for the finger stimulus in the no-instruction group. However they predicted imitation would be more similar between stimulus types in the instructed group, due to increased attention to the object stimulus.

However, although imitative compatibility effects were observed for both stimuli, imitative compatibility effects were equivalent between types in the no-instruction group. This data was interpreted such that, when the spread of attention was too diffuse due to the flash go signal, less attention was focused on the stimulus movement relative to when the cross go signal was used, therefore no difference in imitative compatibility effects was observed between the finger and object stimulus. Equally surprising was that for the instructed group, no automatic effects were found for either stimulus type, despite previous evidence that attention to stimulus movement enhances imitative compatibility effects. It was suggested that when participants are too focused on a particular aspect of the movement (i.e. detecting the difficult oddball trials), cognitive load is increased, and thus cognitive resources required for automatic imitation and differentiating between types of stimulus may not be available. In the current thesis, the role of attention and cognitive load are further explored using similar automatic imitation paradigms.

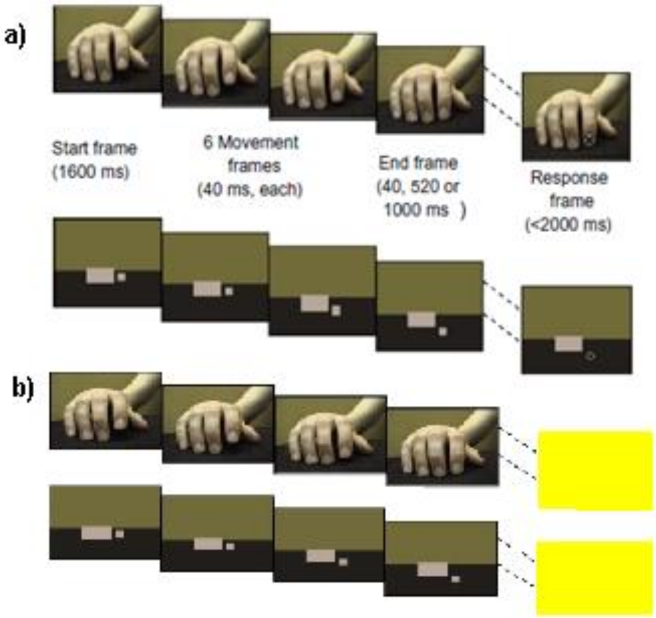

Figure 8: Finger or object stimuli moving in an upwards or downwards direction were presented. At the end of each stimulus movement: **a)** a cross go signal was presented on the moving fingernail/square; **b)** a diffuse yellow flash go signal was presented (Gowen et al., 2010).

In addition, Longo et al. (2008) provided evidence that movement kinematics may only modulate imitation when participants are paying attention to the kinematic aspect of the movement, indicating that an integration of bottom-up and top-down factors are involved in modulating automatic imitation. They used manipulated finger movements to be either biomechanically possible or biomechanically impossible in terms of the movement permitted by joints of the finger. Imitation was present for both possible and impossible movements when no instruction was given. However, when instructed that the observed movements would be either possible or impossible, only possible movements generated automatic imitation effects, suggesting that participants paid closer attention to kinematics following the instructions and therefore inhibited imitation for impossible movements.

In addition to the direct (Bach et al., 2007) and indirect (Longo et al., 2008) evidence that selective attention can modulate the strength of automatic imitation effects (which are thought to reflect MNS activity), an MEG study has also provided evidence that increased attention enhances MNS activity (Muthukumaraswamy and Singh, 2008). They measured beta desynchronization (a component of the mu wave) in the primary sensorimotor cortex (which as discussed in **section 1.4** is thought to reflect the activation of MNs). Beta desynchronization was enhanced in conditions where participants were required to imitate or to perform a maths task (which involved adding up numbers corresponding to which finger moved) following observation of sequences of finger movements, relative to a condition where participants passively observed the movements. **Experiments 1, 2, 3, 4** and **7** were designed to further explore the role of attention in automatic imitation.

1.7.3 Belief

A number of studies have also examined the effects of manipulating participants' beliefs regarding the agency the presented stimulus on the magnitude of automatic imitation effects produced. For example, Stanley et al. (2007) used a dot display following a biologically plausible or implausible velocity profile. Participants were required to move their arm either in a compatible or incompatible direction to the moving dot stimulus. The dot moved with either a biological motion profile or a non-biological motion profile. They found that automatic imitation effects were only produced when participants were instructed that the motion was generated by human movement and absent when they were instructed that the motion was computer-generated, regardless of the kinematic profile of the movement. Similar results have been produced by a number of groups (Liepelt and Brass, 2010; Longo and Bertenthal, 2009), indicating that prior knowledge/beliefs regarding the agency of the stimuli modulates the magnitude of automatic imitation effects produced.

There are two potential interpretations of the influence of belief regarding agency on imitative compatibility effects. The first interpretation is that manipulating belief about agency could cause attention to be drawn to the stimulus in the case of a human belief, or withdrawn from the stimulus in the case of a non-human belief (*attention hypothesis*). In the case of a human belief, increased attention would lead to increased processing of the stimulus, thus causing stronger imitative compatibility effects. In the case of a non-human belief, withdrawn attention would lead to decreased processing of the stimulus and therefore weaker imitative compatibility effects would be produced.

The second interpretation is that imitative compatibility effects are directly modulated by belief, whereby the visuomotor codes generated by the MNS may be up-regulated or inhibited according to one's belief regarding stimulus origin (*top-down belief hypothesis*). According to this hypothesis, if a stimulus is believed to be a human, intentionally produced movement, imitation is altered through up-regulation of visuomotor codes associated with human movement, causing a stronger imitative compatibility effect to be produced. Conversely, in the case of a non-human belief, imitation would be inhibited, reducing or eliminating the imitative compatibility effect.

There have been differences in opinion in the literature regarding these possible interpretations. Longo and Bertenthal (2009) have argued in favour of the attentional hypothesis. In their study, either a virtual hand or real human hand was presented. They found that when the hand was simply referred to as a 'hand', imitative compatibility effects were produced for both stimulus types. However, when the instructions explicitly raised awareness that the stimulus was a 'virtual computer-generated hand', imitative compatibility effects for the virtual hand were reduced. They suggested that the information regarding the virtual nature of the hand drew attention to the artificiality of the virtual hand, causing the reduced effect. They argued that when no instructions are given virtual stimuli may be perceived and processed in the same way as real human stimuli in the brain; with the knowledge of the artificiality of the stimulus remaining in 'subsidiary awareness', meaning that one is implicitly aware of certain aspects of stimuli which are functionally suppressed (Polanyi, 1970). However when attention is drawn to the artificiality of the hand, the knowledge is raised from subsidiary awareness into ‘focal awareness’; thus we no longer perceive the virtual hand as being real. In favour of this explanation, some studies suggest that it is only when participants are specifically made aware to variation in movement (biologically possible/impossible) or stimulus origin (human/non-human) that modulation of imitative compatibility occurs (Longo and Bertenthal, 2009; Longo et al., 2008).

In contrast, Liepelt and Brass (2010) have argued in favour of the top-down belief hypothesis which posits that the human MNS is tuned to the perception of ‘intentional agents’. In this paradigm, they used an identical stimulus consisting of a hand in a leather glove executing finger lift movements. Participants were initially presented with illustrations of either a human hand or a wooden analogue hand wearing the glove. They found that participants who believed that the hand was human exhibited a stronger automatic imitation effect, relative to participants who believed that they had interacted with a wooden hand. They argued that as reduction in imitation occurred even though the gloved hand could be interpreted as either biological or non-biological (and would perhaps be more plausibly interpreted as biological), it was more likely caused by the observer attributing the movement as being intentionally/non-intentionally produced, as opposed to an attentional explanation. If this interpretation is correct, it would support the idea that the MNS is tuned to represent biological stimuli to a greater extent than non-biological stimuli. This interpretation is supported by Castelli et al. (2000) findings that non-biological stimuli can induce activity in the STS when attributed a mental state, suggesting that when a non-biological movement is believed to represent an intentionally produced movement, the movement may be processed in the brain in a similar way to human movement. Alternatively, it has been suggested that these results could be explained by differences in attention or ‘perceptual selection’ of stimulus features. That is, when participants thought it a wooden hand they may have attended to the kinematics of the movement more than the moving effector causing the reduction in imitative compatibility effects, due to less attention being focused on the effector being moved (Heyes, 2013).

There have been some discrepancies in studies of the role of belief regarding agency in automatic imitation. For example, Press et al. (2006) found no evidence of an effect of belief regarding agency. In this experiment, participants observed human or robotic hand movements and were instructed in one session that movements were human generated and in another session that they were computer generated. They found that the magnitude of automatic imitation effects was not influenced by the belief instructions, despite the fact participants’ questionnaire responses indicated that belief regarding agency had been effectively manipulated. On the contrary, automatic imitation was modulated by bottom-up factors i.e. whether the stimulus possessed human or robotic properties, such that the effects were stronger for human relative to the robotic stimulus. In a recent study by Klapper et al. (2014) participants were instructed either that the stimulus hand was created using either human motion capture or that the hand was created by computer animation. This study replicated Press et al. (2006) findings that instructions regarding agency do not influence automatic imitative tendencies when stimulus appearance and kinematics are human-like.

One explanation for this discrepancy is that belief manipulations might operate on an implicit level, only having a pronounced effect on the motor system when the stimulus is relatively ambiguous. In other words, when agency of the stimulus being presented is ambiguous participants may be more likely to be susceptible to the manipulation. For example, it may be more plausible to believe prior information regarding the agency of a gloved hand; however, when observing a stimulus which clearly appears to be a human or robotic hand, the instructions may not be convincing enough to modulate imitative compatibility effects. Similarly, it may be more plausible to believe that an ambiguous dot stimulus movement has been generated by a human movement, than to believe that a robotic movement was generated by a human movement. Thus it is possible that even if participants ‘believe’ a stimulus to be of biological or non-biological origin, this top-down information may have less weighting when bottom-up information is unambiguous.

The literature described provides evidence that the magnitude of automatic imitation produced is modulated by belief regarding the agency of the observed movement, even when the observed stimulus is physically identical. The question of exactly how belief modulates automatic imitation remains unclear, and **experiments 5, 6, 8** and **9** of the work presented in this thesis were designed to further explore this issue.

1.7.4 Summary of factors influencing automatic imitation

In summary, the studies discussed in this section indicate that imitation is influenced by number of top-down influences, including social attitudes, attention and belief. The outlined studies show that magnitude of automatic imitation effects produced for biological versus non-biological stimuli is dependent on these factors. However, this section also highlights the importance of controlling for potential confounds such as spatial compatibility and unmatched stimulus salience, as only imitative compatibility effects that are independent of spatial compatibility and matched for stimulus salience can support the view that imitative processes are biologically tuned. It is likely that an interplay between bottom-up and top-down factors could account for the fact that some studies have documented preferential processing of biological stimuli, while others have documented equivalent effects for biological and non-biological stimuli. In line with this, a number of proposed models of mimicry suggest that it is likely that an integration of bottom-up and top-down signals takes place, which may control the extent to which mimicry behaviour is overtly expressed based on agency cues (Wang and Hamilton, 2012; Gowen and Poliakoff, 2012). These models will be described in the **section 1.8**.

1.8 Theoretical models of automatic imitation

Exactly how bottom up and top factors influence imitative compatibility/overt motor mimicry is still an open question, however a number of possible models have been proposed. Recent neuroimaging studies have been conducted, which indicate that the medial prefrontal cortex (mPFC), as well as the temporoparietal junction (TPJ) are key regions involved in the control of mimicry (Brass et al., 2001a; Brass et al., 2005). These brain regions are activated during brain imaging studies of automatic imitation (Brass et al., 2009) and lesions in these regions are associated with disrupted control of automatic imitation (Spengler et al., 2010c; Brass et al., 2003). Conversely, stimulation to the right TPJ has been shown to enhance the ability to control imitation, as indexed by a reduced tendency to imitate by inhibiting pre-potent motor representations of observed incongruent movements (Santiesteban et al., 2012a). In addition, stronger activations in mPFC and TPJ were observed when participants were required to inhibit their natural tendency to mimic in incompatible trials (Brass et al., 2005).

Wang and Hamilton (2012) have developed the social top-down response modulation (STORM) model. They suggest that mimicry occurs through the MNS pathway developed through the ASL model of imitation (Heyes, 2001), and the MNS interacts with the mPFC/TPJ (‘mentalising system’). Wang and Hamilton (2012) pointed out that there are three possible models for mimicry: 1) the mimicry information from the MNS may feed up to the mentalising system enhancing simulation of the other person (simulation model) **(Figure 9, arrow A)**, 2) social judgements from the mentalising system may be used to control the implentation of mimicry (i.e. a top-down control mechanism most likely implemented by the mPFC) **(Figure 9, arrow B)** or 3) there may be no interaction between the MNS and mentalising system, thus the control of mimicry could be mediated by existing ‘domain-general processes’ (i.e. associative learning and general mechanisms of selective attention).

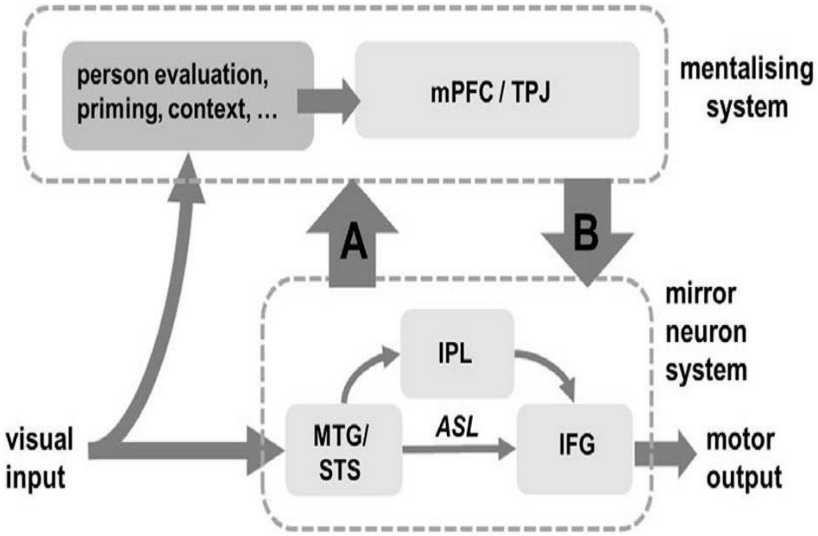

Figure 9: ‘STORM’ model of mimicry (Wang and Hamilton, 2012)

The STORM model is based on evidence that inhibition mimicry is dependent on higher level cognitive and affective procceses including social context and cues such as eye gaze and social status (Wang et al., 2011a; Kampe et al., 2003; Zink et al., 2008), processes which have also been linked with the mPFC. The involvement of the mPFC is also supported by a recent fMRI study in which participants performed a hand movement imitation task. Wang et al. (2011a) previously reported that direct eye contact enhanced imitative compatibility effects. In a subsequent fMRI study, they found the automatic imitation task activated the MNS, while direct gaze and inhibition of mimicry activated the mPFC (Wang et al., 2011b). There was an interaction between eye gaze (direct or averted) and whether mimicry was inhibited or enhanced, suggesting that in line with STORM model, the mPFC modulates mimicry implemented by the MNS. This finding supports Brass et al. (2009) hypothesis that mimicry overlaps with higher social cognitive abilities at a neural level. In addition, using a dynamic causal modelling analysis which is designed to explore the functional connectivity of these regions Wang et al. (2011b) found that there was a strong connectivity between the IFG and the mPFC, suggesting the mPFC may constantly exert top-down control on the MNS. These findings support the idea that mimicry requires higher cognitive control beyond the MNS (Brass et al., 2009; Southgate and Hamilton, 2008).

The STORM model of mimicry is compatible with Heyes and Bird (2007) model which suggests that visuomotor action control may operate automatically. However according to this model ‘moderating factors’, such as sensorimotor experience/learning, ‘input factors’ (variables affecting stimulus processing such as stimulus salience), and ‘output factors’ (top-down processes) **(Figure 10; right panel)** may influence behaviour. These moderating factors may be important in determining whether a mirroring response is overtly expressed or inhibited. Spengler et al. (2010b) proposed that such factors might influence behaviour in one of two ways: 1) through an activating route which enhances the sensory representation (as shown by the green line in **Figure 10; left panel**) or 2) through an inhibitory route which inhibits the motor representation (as shown by the red line **Figure 10; left panel**). As discussed in **sections 1.7** and **section 1.7.1,** some evidence (e.g. the reduced control of imitative tendencies in patients with frontal lobe lesions) suggests that the inhibitory route is more likely.

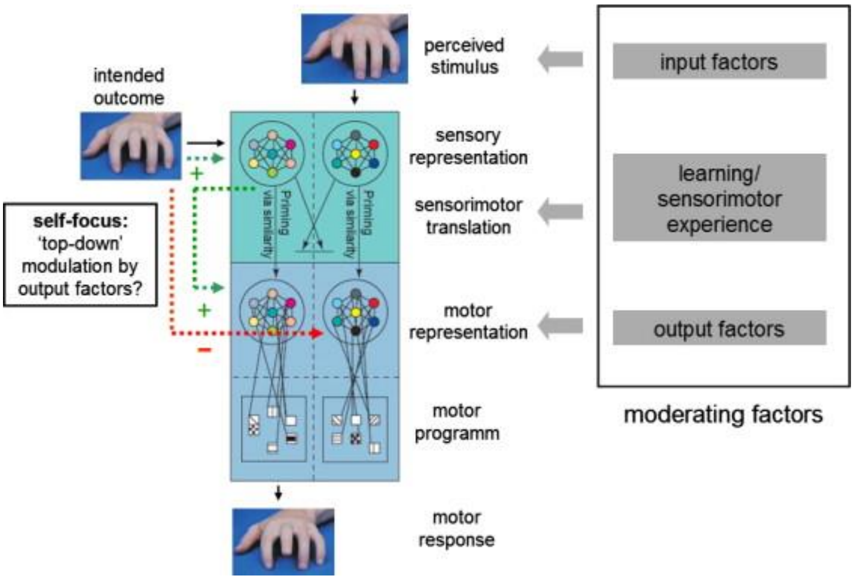

Figure 10: Model of how moderating factors may affect automatic imitation (Spengler et al., 2010b).

Gowen and Poliakoff's (2012) recent model is particularly relevant to the current work, as it can potentially explain why a number of studies have found a human bias while some other studies have not. The model comprises of two routes **(Figure 11)**. The first route is a 'visuomotor route' which translates observed visual information into action via one of two mechanisms 1) a low level, relatively automatic form of imitation which is dependent on bottom-up factors such as stimulus saliency and on experience/learning, or 2) a higher level which is dependent on goals. It is suggested that both biological and non-biological stimuli would be processed within the visuomotor route. The second route is a top-down modulation route via the prefrontal cortex.

According to Gowen and Poliakoff's model, the prefrontal cortex would process top-down information regarding appearance, kinematics, instructions, context and attention and consequently modulate imitation via the IFG, an area consistently associated with inhibition of mimicry (Brass et al., 2005; Bien et al., 2009). However, it is suggested that the paracingulate cortex, a part of the mPFC which has been implicated in theory of mind and self-referential processing, may act as a 'comparator' in situations where our predictions of a stimulus do not meet our expectations (Gowen and Poliakoff, 2012). Stanley and colleagues (2010) investigated neural activity using fMRI during a task in which participants were informed that the observed stimulus was either a human or computer-generated stimulus. They found that the ventral paracingulate cortex was active during the human instruction suggesting that this region processes stimuli considered 'similar' to oneself. In contrast, the dorsal paracingulate cortex was active when the stimulus and instructions were incompatible suggesting that this area may process information when the biological nature of the stimulus is considered ambiguous, or there is a conflict between instructions and stimulus appearance. Gowen and Poliakoff's model posits that if attention is drawn to the non-biological nature of the stimulus, imitation via the visuomotor route may be inhibited either via the STS, or through direct connections from the paracingulate cortex to the visuomotor route. On the other hand, if attention is drawn to the human nature of the stimulus, the ventral paracingulate cortex might become active, enhancing imitation via the same connections.

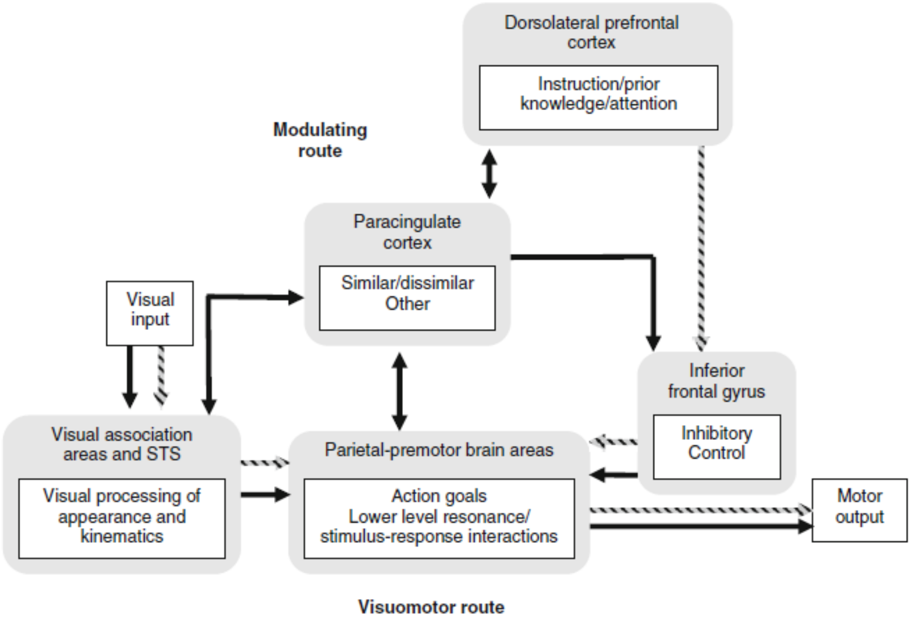

Figure 11: Gowen and Poliakoff (2012) dual route model of mimicry.

A recent fMRI study suggests that the right temporoparietal junction (rTPJ) might constitute a specialised neural circuitry that controls imitation of movements which appear to be and are believed to be human movements (Klapper et al., 2014). In this study, they used an automatic imitation paradigm and manipulated both bottom-up (by using both human and robotic stimuli) and top-down (by giving prior instructions that the observed movements were created using human motion capture or a computer animation algorithm) agency cues. They found that automatic imitation was equivalent when one or both cues to agency were present, but was reduced when both cues were absent. By contrast, the rTPJ showed sensitivity to the presence of both agency cues (i.e. when the hand both looked like and was believed to be human). However, the authors discuss the fact that the rTPJ is unlikely to be the sole 'control centre' for imitation, based on the fact that the anterior mPFC has been implicated in the control of imitation based on eye gaze (Wang et al., 2011a) and paracingulate cortex and dorsal prefrontal cortex have been implicated in control of imitation based agency cues (Gowen and Poliakoff, 2012). Furthermore, they found preliminary (due to the exploratory nature of the fMRI analysis used) evidence that the rTPJ and the prefrontal cortex are functionally coupled.

1.9 The MNS and automatic imitation in ASC

ASC is a lifelong, genetically-based neurodevelopmental disorder, which is diagnosed on the basis of the presence of three core behavioural abnormalities: atypical social development, language and communication impairment, and stereotyped interests/repetitive behaviours (American Psychiatric Association, 2000). The ‘broken mirror’ theory of ASC has gained significant attention in recent years. This theory claims that alterations to the MNS during development causes the symptoms of ASC (Iacoboni and Dapretto, 2006; Ramachandran and Oberman, 2006). Broken mirror theorists have argued that a MNS dysfunction could potentially explain the imitative deficits documented in ASC (Rogers and Pennington, 1991; Williams et al., 2004). Furthermore, since the functions that are disrupted in ASC appear to greatly overlap with proposed functions of the MNS, such as theory of mind, it has been hypothesized that dysfunctions of the MNS could lead to the deficits in social interaction that are characteristic of ASCs.

This hypothesis provoked a flurry of studies due to its intuitive appeal; however, on the whole this theory has not been enthusiastically accepted. Southgate and Hamilton’s critical review in 2008 argued that the broken mirror theory of ASC was premature, and further research would be required in order required to fully understand the relationship between the MNS, imitation and ASC. A number of observations in ASC are incompatible with a global impairment of the MNS. For example, several studies have shown that explicit goal-directed imitation is not impaired in ASC (Rogers et al., 1996; Stone et al., 1997; Hobson and Lee, 1999; Williams et al., 2004; Wild et al., 2012). Furthermore, a number of studies have reported intact automatic imitation effects (Gowen et al., 2008; Bird et al., 2007; Press et al., 2010). As will be outlined in the following paragraphs, investigations of the integrity of the MNS in ASC using a number of different methods have also produced conflicting results.

A number of research groups have observed typical mu suppression in response to self-performed actions, but significantly reduced suppression in response to observed actions in ASC (Oberman et al., 2005; Bernier et al., 2007; Martineau et al., 2008), providing initial evidence for an impairment of the MNS in ASC. In addition, the degree of impairment of imitation skills in ASC participants was found to be positively correlated with the degree of mu suppression (Bernier et al., 2007). However it has been pointed out by Hamilton (2012) that these reports are based on simple main effects, and none of the studies report a conclusive group by condition interaction in which ASC participants show mu suppression when performing an action, but do not when observing actions. Additionally, two studies have found no difference in mu suppression in ASC (Fan et al., 2010; Raymaekers et al., 2009).Thus the evidence suggesting that mu rhythm suppression in ASC is atypical is inconclusive.

TMS with MEP studies have shown that the excitability of the primary motor cortex in individuals with ASC was significantly lower than matched controls, whilst observing video clips of meaningless finger movements when the hand was oriented as if it belonged to the participant, but showed normal MEP enhancement when observing a hand oriented as if it belonged to someone else (Theoret et al., 2005). However, it has been argued that this finding is difficult to interpret, suggesting a possible impairment in self-body image rather than in social mimicry. A more recent study by Enticott and colleagues (2012) reported that ASC participants did not show the same MEP enhancement as neurotypical participants when watching a hand grasp a mug relative to watching a static hand, indicating a possible MNS abnormality in ASC.

Two studies have attempted to measure muscle activation in individuals with ASC using electromyography (EMG) methods, providing mixed evidence. Cattaneo and colleagues (2007) recorded EMG from the mylohyoid muscle while neurotypical and autistic children picked up food to either eat or place upon their shoulder, or observed someone performing the same task. They reported that the mylohyoid muscle was not activated in autistic children during the anticipatory grasping phase of performing the action, but was in neurotypical children. Furthermore, autistic children did not show mylohyoid muscle activity when watching an action being performed, whereas neurotypical children did. However, Pascolo and Cattarinussi (2012) were unable to replicate this finding, observing no anticipatory mylohyoid activity for ASC or for neurotypical children. In addition, Southgate et al. (2009) argued that Cattaneo et al.'s (2007) findings might be better explained by known difficulties in motor planning (Gowen and Hamilton, 2012) rather than a MNS impairment.

Significant discrepancies have also arisen between different functional magnetic resonance imaging (fMRI) studies. In one study, the ASC participants displayed significantly weaker or completely absent activity in the right parietal lobe during non-imitative action execution and normal activity in the IFG during imitation (Williams et al., 2006). Another research group also found atypical patterns of activity representing the MNS in ASC when imitating or observing facial expressions; and further that the amount of activity observed correlated to the severity of symptoms in ASC (Dapretto et al., 2006). However, in contrast to Williams and colleagues (2006) they found normal activity in parietal areas and reduced activity in the IFG (Dapretto et al., 2006). Confusingly, Martineau et al. (2010) found greater activation of the IFG in participants with ASC than in neurotypical participants. In addition, normal activations in MNS regions in individuals with ASC have been reported by a number of groups during observation and execution of hand movements (Dinstein et al., 2010; Marsh and Hamilton, 2011) and emotional facial expressions (Ashwin et al., 2007; Schulte-Rüther et al., 2011) suggesting the MNS is not dysfunctional in ASC.

Magnetoencephalography (MEG) studies have also provided inconclusive evidence. For example, in a study in which participants were required to observe still images of lip forms, it has been observed that ASC participants' pattern of cortical activation in the occipital cortex, superior temporal cortex, and inferior parietal lobe was equivalent to control participants. However, activations in the frontal lobe and primary motor cortex were weak in comparison with the control group (Nishitani et al., 2004). However, these results were based on a small sample size of 8 participants, and so should be interpreted with caution. Furthermore a conflicting MEG study has demonstrated that the primary motor cortex was activated to the same extent in autistic individuals relative to healthy individuals following observation of hand actions (Avikainen et al., 1999).

In addition to the conflicting evidence regarding the integrity of the MNS in ASC, behavioural evidence has been inconsistent. A number of recent studies have demonstrated that individuals with ASCs show an intact and even enhanced automatic imitation effect (Gowen et al., 2008; Bird et al., 2007; Press et al., 2010), suggesting that the MNS is intact in ASC. The first experiment to investigate automatic imitation in ASC using EMG experiment suggested a possible impairment (McIntosh et al., 2006). They measured the muscular activity of the face while participants observed facial expressions, and found that individuals with ASC showed less automatic expression-compatible muscle activity compared to healthy control participants. However, these results did not take into account that a reduced sensitivity to social cues is well-documented in ASC, thus autistic participants may not have generally attended to stimuli in the same way as healthy participants.

A reduced sensitivity to biological motion has been documented in ASC (Miller and Saygin, 2013) and a number of lines of evidence suggest that social stimuli are not granted the same priority in ASC as in neurotypical participants. For example, when observing static photographs of social situations, children with ASC tended to look more at the background than the face or bodies of the people in the photographs (Riby and Hancock, 2009). Similarly, when observing video clips, it has been observed that participants with ASC tend to fixate less on people’s faces and eyes than other areas (Klin et al., 2002; Nakano et al., 2010). Falck-Ytter et al. (2012) found that when children observed video clips of an actor making eye contact with the camera, then looking or pointing at an object, participants with ASC looked at the object less. Furthermore, Bird et al. (2006) have demonstrated that in contrast to neurotypical adults, participants with ASC do not show increased activity of the fusiform face area when attending to faces, highlighting reduced attentional modulation to faces.

A number of studies have also shown that there is a reduced sensitivity to social cues in ASC. Pierno et al. (2006) observed that children with ASC fail to understand motor intentions of others from gaze, as they fail to use a models gaze to plan their own actions, suggesting that the ability to read another’s goals and intentions is abnormal in ASC. Similarly, Vivanti and colleagues (2011) found that individuals with ASC showed reduced sensitivity to social cues conveyed by the demonstrators face, relying on the objects or actions involved in the demonstration. Difficulties in integrating the social cues provided by the demonstrator have also been reported in other studies (D’Entremont and Yazbek, 2007). These findings indicate that differences in automatic imitation reported in ASC in studies examining facial expressions, could be due to impaired sensitivity to social and communicative cues and differences in face-processing.

Bird et al. (2007) used simple hand movements to investigate automatic imitation in ASC in order to avoid these issues. Participants were required to either open or close their hand as soon as the observed stimulus hand began to move. They found that participants with ASC showed equivalent or even enhanced automatic imitation effects compared to controls, suggesting that MNS is intact in ASC. Another study by Gowen et al. (2008) using vertical or horizontal arm movements while congruent or incongruent arm movements were presented, found that ASC participants and matched controls produced an equivalent automatic imitation effect. In agreement with the above studies, Press et al. (2010) found intact imitation of emotional facial expressions in ASC. Importantly, this finding of intact automatic imitation is incompatible with the idea of a global impairment of the MNS in ASC. In addition, the fact that hyperimitation has been documented in ASC (Spengler et al., 2010a; Tardif et al., 2007), as well as reports of echolalia and echopraxia (Ford, 1991), indicates that the problem in ASC may lie in inhibition of imitation.

In summary, although some lines of evidence suggest the MNS might be abnormal in autistic individuals, the evidence of ‘broken mirrors’ in ASC provided to date is weak. The previously described studies examining MNS activity in ASC show a highly inconsistent pattern. These findings cannot be fully accounted for by global deficit in the MNS, as proposed by broken mirror theorists. Moreover, there is a growing body of evidence supporting the theory that that it is the ability to control automatic imitation that is atypical in ASC (Hamilton, 2008). This theory will be described in further detail in the following section.

1.9.1 Top-down modulation hypothesis of ASC

A recent model by Hamilton (2008) posits that conflicting results in studies of imitation in ASC can be explained if there are two routes for imitative behaviour: 1) an intact indirect route for emulation and planning of goal-directed actions, supported by findings that ASC participants show intact goal-directed imitation and may rely to a greater extent on the goal-directed imitation pathway (Gowen and Hamilton, 2012) and 2) a direct route for true imitation and automatic imitation. Hamilton (2008) proposes that individuals with ASCs may exhibit dysfunctional top-down modulation (via the mPFC) of the direct route. This theory implies that imitation of the goal of an action is not socially motivated but is based on achieving the goal, thus goal-directed imitation is not impaired in ASC. On the other hand, automatically imitating requires modulation based on social control signals that might only occur if one is socially motivated to engage with the interacting partner. Thus, atypical imitation in ASC may reflect a lack of motivation to engage socially.

Failure of top-down modulation of imitation in ASC could account for many of the differences in imitation observed in ASC. For example, it has been observed that automatic imitation in individuals with ASC was not influenced by pro-social or anti-social priming (Cook and Bird, 2012). This fits in with the idea that people with ASC may have difficulty with appropriately modulating levels of imitation based on social contexts. Similarly, Grecucci et al. (2012) tested the ability to imitate finger movements which were preceded by neutral or emotional facial expressions, and found that while imitation was equivalent for ASC and neurotypical participants when hand movements were performed after neutral expressions, participants with ASC did not show enhanced imitation for hand movements performed after emotional facial expressions. This study suggests that imitation abilities are intact; however, imitation is not modulated by emotional/social contexts in ASC.

In addition, some groups have found that in contrast to neurotypical children, children with ASC responded more to a robotic movement than human movement (Pierno et al., 2008), whereas others have observed that individuals with ASC showed a greater automatic imitation in response to human movement relative to robotic movement (Bird et al., 2007). It is plausible that abnormal top-down modulation in ASC could explain these conflicting findings. If, as proposed by Gowen and Poliakoff (2012), the top-down modulation route is responsible for judging whether a stimulus is similar or dissimilar to oneself, if it is correct that top-down control of imitation is dysfunctional in ASC, autistic individuals may be unable to correctly differentiate between biological and non-biological stimuli, leading to the lack of agreement in the aforementioned studies.

There is also evidence of reduced motor and emotional contagion in ASC. For example, Helt et al. (2010) have shown that children with ASC are less susceptible to contagious yawning than neurotypical children. Contagious yawning is thought to be a form of emotional contagion which may arise due to motor mimicry. Similarly, Tetteroo et al. (2012) have shown that autistic children do not mimic expressiveness in game play, in the same way as typically developing children. In addition, Becchio et al. (2007) observed that autistic children appear to be unaffected by motor contagion. It is possible that individuals with ASCs may not perceive (therefore exhibit) mimicry during social interactions due to reduced social attention or difficulties in emotional perception (Chevallier et al., 2012). This may explain a lack of social affiliation with others developed through motor mimicry, leading to or exacerbating the socio-communicative problems of autistic individuals. Interestingly, a recent study showed that when a fixation cross is used to cue attention to faces there was no difference in imitation of facial expressions between ASC and neurotypical participants (Hadjikhani et al., 2004). Similarly, when forced to pay attention to the action, automatic imitation effects in ASC do not differ from controls (Bird et al., 2007; Press et al., 2010). This suggests that, in line with an impairment in top-down modulation of imitation, when participants with ASC are forced to pay attention to stimuli that they might naturally show reduced attention to relative to controls, imitation is normalised.

In addition, in healthy individuals, imitation relies on normal processing of social and communicative cues as well as the interacting partner’s goals and intentions in order to correctly control imitation, and these abilities are known to be impaired in ASC. Such difficulties could therefore lead to abnormal top-down modulation in ASC. If individuals with ASCs are unable to control mimicry, this may also result in excessive mimicry in some cases, explaining the echolalia and echopraxia exhibited by some autistic individuals (Grossi et al., 2013).

Atypical top-down modulation is likely to occur due to atypical function of MNS and frontal control brain regions (PFC and TPJ), or atypical connectivity between these regions. Interestingly, Klapper and colleagues' (2014) recent finding that the rTPJ might constitute a specialised control centre for human movements is more consistent with the top-down modulation hypothesis than it is with a deficit in the MNS. The TPJ is also activated during mental and spatial perspective taking, suggesting that control of imitation and perspective taking abilities might share cognitive mechanisms, such as the ability to differentiate between ‘self’ and ‘other’. It has been proposed that since the mPFC and TPJ are active during inhibition of mimicry and mentalising (Van Overwalle and Baetens, 2009), that these processes might be closely associated (Brass et al., 2009). In line with this, Spengler et al. (2010a) found a strong correlation between control of mimicry, and mentalising and visual perspective taking in both healthy patients and patients with prefrontal and TPJ lesions. Similarly, Santiesteban et al. (2012b) found that training participants to inhibit the tendency to mimic caused improved performance on a visual perspective taking task relative to a group with no imitation-inhibition training. Interestingly, Spengler and colleagues (2010a) observed hyper-imitation (suggesting reduced control) of hand actions in autistic participants relative to controls, which was correlated with reduced activity of the mPFC and TPJ (areas known to be key to the control of imitation). This suggests that there is a correlation between socio-cognitive functioning and the ability to control/inhibit automatic imitation, such that participants who performed worst in mentalising tasks were also the least able to inhibit automatic imitation.

It has also been observed that the mPFC is abnormal in ASC (Kennedy et al., 2006; Gilbert et al., 2009), making it plausible that faulty top-down control of mimicry might account for abnormal mimicry behaviour in ASC. In addition, fMRI studies have suggested that functional connectivity between the mPFC and MNS is significantly weaker in ASC (Kana et al., 2014), and that there is reduced connectivity between frontal and posterior areas in ASC during mentalising tasks (Castelli et al., 2002; Spengler et al., 2010a). Both the mPFC and rTPJ are also activated during mental state attribution, such as beliefs, desires, and intentions (Van Overwalle and Baetens, 2009) and atypical activations in these regions have been associated with atypical processing of social information in ASC (Marsh and Hamilton, 2011; Castelli et al., 2002). It has also been proposed that the rTPJ is selectively involved in representing the beliefs of others (Saxe and Powell, 2006); which individuals with ASC fail to do (Baron-Cohen et al., 1985; Senju et al., 2009). Typical development of mental state reasoning abilities is associated with increasing selectivity of TPJ responses (Gweon et al., 2012) and rTPJ activation in adulthood during automatic imitation tasks overlaps with belief reasoning tasks (Spengler et al., 2009). Therefore it is possible that imitative problems may be linked to the lack of ability to spontaneously attribute mental states.

One interesting question is whether the proposed atypical function/connectivity of these brain regions is caused by a genetic predisposition or an acquired deficit (e.g. due to the fact individuals with ASC are not socially motivated, thus are less likely to acquire links between social cues and MNS activity). Future studies in which individuals with ASC are 'trained' in top-down modulation of imitation could tease apart these two possibilities, as a genetic predisposition would be unresponsive to such training.

1.9.2 Empathy and imitation

Empathy is the experience of understanding another person's emotions and sensations from their perspective. It is an important ability as it allows individuals to share the affective states of others, predict the actions of others, and stimulates pro-social behaviour. It is generally agreed that there are two distinct components of empathy (Davis, 1983): 1) cognitive empathy (the ability to intellectually understand another's experience/perspective or feelings) and 2) affective/emotional empathy (the ability to empathize and respond emotionally/be affected by another's emotional state).

It is generally assumed that a relationship between empathy and imitation exists; however, there is limited empirical evidence to support this relationship (Baird et al., 2011). Only a few studies have actually directly explored the relationship between individual differences in empathy and imitation. Chartrand and Bargh (1999) suggested that the cognitive component (perspective taking) is more relevant to mimicry. In line with this hypothesis they observed that perspective taking, as measured by the 'perspective taking' scale scores on Davis' (1983) Interpersonal Reactivity Series (IRI) empathy questionnaire, was positively correlated with frequency of motor mimicry in a semi-naturalistic environment. However, they found no correlation between emotional empathy scores and motor mimicry. In contrast, using EMG to measure motor mimicry of facial expressions, Sonnby–Borgström (2002) found that individuals with high affective/emotional empathy as measured by the questionnaire measure of emotional empathy (QMEE; Mehrabian and Epstein, 1972) showed a greater degree of mimicry of facial expressions than those with lower emotional empathy scores. It is consequently unclear which component of empathy (cognitive or affective) is related to imitation. In addition, Baron-Cohen and Wheelwright (2004) have argued that in most instances the cognitive and affective components of empathy co-occur and thus cannot easily be separated.

Given that the MNS is the proposed neural correlate for imitation, due to the assumed relationship between imitation and empathy, the MNS has also been proposed as the neural correlate of empathy by some scholars (Carr et al., 2003; Gallese, 2003; Leslie et al., 2004). In support of this proposal, neuroimaging studies have reported correlations between MNS activation (most commonly based on increased activation of the IFG) and self-reported empathy scores (Davis's IRI) (Gazzola et al., 2006; Kaplan and Iacoboni, 2006; Pfeifer et al., 2008; Jabbi et al., 2007). However, in one study there was a negative correlation (Kaplan and Iacoboni, 2006) between the personal distress scale of the IRI (a subset of emotional empathy) and MNS activation while in two other studies there was a positive correlation (Pfeifer et al., 2008; Jabbi et al., 2007). In contrast, Gazzola et al. (2006) found a positive correlation between perspective taking (a subset of cognitive empathy) and the MNS. Thus, neuroimaging observations have provided mixed results in terms of the direction of the correlation and the components of empathy involved.

Given the limited evidence supporting the link between imitation/the MNS and empathy, the view that MNS underpins empathy has been more recently challenged (Decety, 2010). Further research will be required to fully understand the relationship between imitation and empathy.

1.9.3 Empathy in ASC

Although impaired empathy is often considered to be a characteristic feature of ASC (Baron-Cohen and Wheelwright, 2004; Blair, 2008), surprisingly this relationship has not been conclusively proven. Evidence to date suggests that the relationship between empathy and the ASC is highly complex. Most of the evidence supporting an empathy impairment in ASC actually stems impairments in theory of mind (ToM), which is defined as the ‘ability to understand the feelings, intentions, and motivations of others’ (Premack and Woodruff, 1978). This definition is extremely similar of the definition of cognitive empathy i.e. the ability to intellectually understand another’s experience (Duan and Hill, 1996). Based on this similarity, the terms ToM and cognitive empathy have often been used synonymously; however studies assessing the relationship between ToM and the different components of empathy have not been carried out, thus it is unclear whether ToM and cognitive empathy are actually equivalent (Rogers et al., 2007). It has long been observed that ToM is impaired in children with ASCs (Baron-Cohen et al., 1985) and this observation has since been replicated repeatedly (see Baron-Cohen, 2000 for a review). Interestingly, 90% of the 40 studies reviewed by Carrington and Bailey (2009) found that the mPFC was activated during theory of mind tasks. Thus, dysfunctional activity/connectivity of the mPFC in ASC is consistent with a theory of mind deficit and the top-down modulation hypothesis of mimicry in ASC. Given that the fact the terms ToM and cognitive empathy have been used interchangeably, many of the empathetic deficits reported in ASC have been based on deficits in theory of mind.

A few studies have assessed emotional empathy in ASC. Shamay-Tsoory et al. (2002) found both emotional empathy and cognitive empathy were impaired in ASC. In contrast, two other groups found that cognitive empathy was impaired in ASC, while emotional empathy was intact relative to controls (Rogers et al., 2007; Dziobek et al., 2008). In support of Baron-Cohen's (2011) suggestion that individuals with ASC lack both cognitive and affective empathy, self-reported empathy scores tend to be low in autistic populations, and self-reported levels of autistic traits measured using the autism quotient (AQ) questionnaire scores (Baron-Cohen et al., 2001) are negatively correlated with levels of empathy measured using the Empathy Quotient (EQ; Baron-Cohen and Wheelwright, 2004), a questionnaire that does not separate questions into cognitive and affective empathy components, but assigns an overall empathy score.

Empathy has been associated with individual variation with how strongly brain regions involved in one's own actions, emotions and sensations, are activated while viewing those of others. These neural areas include: the premotor cortices (Keysers and Gazzola, 2009), the primary and secondary somatosensory cortices (Keysers et al., 2010), the insula and the anterior/mid cingulate (Wicker et al., 2003; Jabbi et al., 2007; Bastiaansen et al., 2009; Lamm et al., 2011). Interestingly, results of a neuroimaging study suggest that although psychopaths have reduced spontaneous activations of these regions when simply witnessing pain in comparison to a healthy control group, these group differences were significantly reduced when psychopaths were explicitly instructed to empathize. Keysers and Gazzola (2014) have argued that this finding begs the question whether in psychiatric disorders which are associated with a lack of empathy such as psychopathy or ASC, reduced empathy is due to a lack of spontaneous propensity to empathize (as opposed to a lack of ability to empathize). They also raise the issue that a number of self-measures of empathy include questions which do not distinguish between empathetic ability and propensity. For example, the following statement taken from the EQ questionnaire (used in the current experiment): 'I can tune in to how someone else feels rapidly and intuitively" include both empathetic ability ('can') and propensity ('rapidly', 'intuitively'). The fact that simply changing instructions can boost these low spontaneous activations reveals that empathy is not an entirely automatic process. In addition, another study has shown that psychopaths show significantly reduced amygdala activations during fear conditioning compared to a control group, however when asked to explicitly attend to the threat stimulus, activations normalized (Larson et al., 2013). These findings suggest empathy may depends on attention and/or motivation, which further leads to the hypothesis that the degree to which attention is automatically captured by social stimuli might predict an individual's propensity for empathy (Keysers and Gazzola, 2014). If attention to social stimuli predicts propensity for empathy this might explain why individuals with ASC tend to have low EQ scores.

In the current thesis, we aimed to further examine the seemingly complex relationship between empathy, autistic traits and imitative compatibility effects.

1.10 Aims and objectives

The primary aim of this thesis was to provide further evidence that 'automatic' imitation is modulated by the top-down factors of attention and belief, using a movement compatibility automatic imitation paradigm. This research ultimately aimed to develop a paradigm that could potentially be used to directly test the top-down modulation hypothesis in ASC populations. This would be useful in disambiguating the opposing proposals of researchers supporting the broken mirror theory and those proposing that the top-down control of imitation is atypical in ASC. In addition, even if the control of imitation turned out not to be atypical in ASC, a greater understanding of the factors that modulate imitative tendencies would be useful in improving the effectiveness of interventions aimed to increase imitation in ASC. Such interventions have proven to be useful in improving language development (Ingersoll, 2008; Ingersoll and Lalonde, 2010). Furthermore, guides used to help practitioners design programs for children with ASC typically include recommendations for the development of imitative skills (Lovaas et al., 1981; Maurice et al., 1996).

Specifically, this current thesis aimed to address the following questions:

1. How is imitation modulated for biological and non-biological stimuli?

Initially, in **experiment 1** we aimed to examine whether selective attention to stimulus movement modulates the difference in imitative compatibility effects between biological and non-biological stimuli. An easy visual dual task was added that was designed to draw attention to stimulus movement. However, unexpectedly, the visual dual task removed imitative compatibility effects for the finger stimulus. Therefore, in **experiment 2** we added an auditory dual task in order to explore whether the removal of imitation was due to general high cognitive load, or the fact that the visual dual task and imitation task both accessed the visual modality.

Furthermore, in **experiments 3 and 4** we aimed to examine whether imitative compatibility effects were more likely to be significant when trials are presented in separate blocks as opposed to randomly intermixed with a block of trials, due to differences in attention, or due to a carry-over of agency/implicit belief based on the order in which stimuli are presented.

We also aimed to explore whether the spread of attention, caused by the go signal used, modulates the magnitude of the imitative compatibility effects produced by comparing a diffuse and focused go signal in **experiment 7**.

2. Does the belief that an ambiguous object stimulus movement was generated by a human movement strengthen imitative compatibility effects?

If so, we aimed to examine exactly how a human belief modulates imitative compatibility effect. A human belief could modulate imitative behaviour in one of two ways: 1) belief could increase attention to the stimulus causing increased processing of the stimulus movement, thus stronger imitative compatibility effects or 2) the top-down belief that the stimulus is of human origin could directly up-regulate visuomotor codes generated by the MNS. **Experiments 5, 6 8 and 9** were designed to distinguish between these two possibilities.

A secondary aim of this thesis was to explore whether there is a relationship between empathy/autistic traits and imitative compatibility of finger movements, by correlating self-reported questionnaire measures of empathy and autistic traits with imitative compatibility.

This thesis also aimed to address the methodological issues associated with automatic paradigms, such as controlling for stimulus salience and spatial compatibility. We controlled for stimulus salience by using the same go signal for both biological and non-biological stimuli and matching stimuli for size, dimensions, colour and luminance. We controlled for spatial compatibility by exploring the best way to present stimuli in automatic imitation paradigms, such that a pure imitative compatibility effect can be measured in the absence of other contaminating SRC effects. Since a number of previous studies which have examined the difference in imitation between human and non-human stimuli, as well as studies examining the role of belief and attention in automatic imitation have confounded spatial compatibility and automatic imitation effects, we were interested in examining whether such previously documented effects were true imitative compatibility or whether they were based on spatial compatibility effects.

Chapter Two

Exploring the role of attention in imitative compatibility effects

2.1 Chapter Introduction

In light of Gowen et al. (2010) findings that imitative compatibility effects may be removed if attention is either too focused, or too diffuse, the current project aimed to further investigate the seemingly complex role of attention in imitative compatibility. As discussed in detail in **section 1.6.2**, Gowen et al. (2010) found that the human bias of ’automatic imitation’ disappeared when a ‘X’ cross go signal located on the moving part of the stimulus, was replaced by a diffuse flash go signal. The authors suggested that the diffuse flash go signal introduced a more diffuse spread of attention, thus participant’s attention may not have been drawn to stimulus differences. Therefore in **experiment 1a** we aimed to determine whether the typical human bias could be reinstated using a diffuse flash go signal at earlier SOAs, during the movement of the stimuli. We predicted that imitative compatibility effects would be stronger at earlier SOA’s as attention would be more likely to be focused on the stimulus movement.

Furthermore, Gowen et al. (2010) results suggested that, contrary to its original purpose of directing attention to stimulus movement, the subtle ‘oddball’ detection task was too cognitively demanding, leading to the removal of imitative compatibility effects. Therefore in **experiment 1b**, we explored whether using a significantly easier and more salient version of the secondary visual ‘oddball’ detection task would successfully draw attention to the stimulus, thus producing imitative compatibility effects and further strengthening the human bias.

Following the unexpected finding in experiment 1b, that even a significantly easier and more salient version of the oddball detection task removed imitative compatibility effects for the finger and the human bias; we aimed to investigate whether the removal of imitation was due to high cognitive load or due to the fact both tasks (imitation and the secondary ‘oddball’ detection task) were situated in the same sensory modality (i.e. both tasks were visual). To this end, in **experiment 2** we investigated whether imitative compatibility effects would be present when using an auditory secondary task.

Finally, in **experiment 3**, we continued to explore the theme of attention using a different approach. We examined whether presenting the biological and non-biological stimuli in separate blocks of trials, as opposed to randomly intermixed within a block of trials, modulates the strength of imitative compatibility effects, due to differences in attention (described in further detail in **section 2.3**).

2.1.1 Experiment 1a and 1b - Introduction

Our primary aim in experiment 1a was to investigate whether stronger imitative compatibility effects would be produced for a biological moving finger stimulus relative to a non-biological moving object stimulus in the control group when using a diffuse flash go signal presented at earlier SOAs. Therefore, we altered Gowen et al. (2010) original paradigm by presenting a diffuse flash go signal at earlier SOAs (as opposed to post stimulus movement). We hypothesized that if earlier SOAs influence attention, we would expect imitative compatibility effects to be present. Furthermore we hypothesized that at earlier SOAs which occur during stimulus movement the human bias may be reinstated, as more attention may be directed to the stimuli (and therefore the stimulus differences). If this hypothesis is correct an interaction between stimulus and compatibility should be present, indicating that imitative compatibility effects were significantly greater for the finger stimulus relative to the object stimulus. Three variable SOAs were used; one occurred immediately prior to movement onset, one during the movement, and one at movement offset.

In experiment 1b, we aimed to develop an effective attentional manipulation to further strengthen imitative compatibility effects, by directing attention towards stimulus movement. As in Gowen et al. (2010), in experiment 1b an ‘oddball’ detection task was used, however the difficulty of the task was significantly decreased, by increasing the visual saliency of the oddball trials, creating an obvious ‘jump’ in the movement. There were three alternative hypotheses for this attentional manipulation. Firstly, if monitoring for oddball jumpy movements drew attention to the differences between the stimuli, we would expect to see further strengthening of the human bias of imitative compatibility effects. If this is the case an interaction between stimulus and compatibility should be present indicating greater imitative compatibility effects for the finger relative to the object stimulus). Furthermore a greater difference in imitative compatibility effects between the finger and object would be present relative to experiment 1a. Secondly, if the manipulation drew attention towards the movement of both stimuli equally, we would expect to see similar imitative compatibility effects for the biological and non-biological stimuli. Thirdly, if imitative compatibility is still absent, this would suggest that high cognitive load cannot explain the absence of imitation in Gowen et al. (2010; Experiment 2b).

Additionally, we aimed to examine the relationship between imitative compatibility effects and self-reported measures of (1) how participants think about the stimuli and (2) empathy. Participants were therefore required to complete an empathy questionnaire and an additional questionnaire consisting of six statements and four questions, which were designed to examine the extent to which participants reported to have attended to and perceived the differences between biological and non-biological stimuli during the experiment.

2.1.2 Methods

2.1.2.1 Participants

In all of the experiments presented in this thesis, participants all had normal or corrected-to-normal vision and were naïve to the purpose of the study. Participants were all self-reported right-handers, wrote with their right hand and were classified as right-handed according to the Edinburgh Laterality Inventory (ELI; Oldfield, 1971) **(Appendix A1)**. Ethical approval for these studies was obtained from the University of Manchester Research Ethics Committee, and participants gave their informed consent to take part.

40 right-handed healthy individuals (23 female), with a mean (±SD) age of 24.45 (±4.93) years were recruited. Participants mean (±SD) Edinburgh Handedness Inventory laterality quotient was 81.71 (±18.24) (where a score of +100 represents absolute right-handedness and a score of -100 represents absolute left-handedness). The study consisted of a single testing session lasting approximately 1 hour, and participants were paid £5 for their participation. Participants were split at random into two testing groups; experiment 1a: control group (n = 20) and experiment 1b: attention-directed group (n = 20).

2.1.2.2 Apparatus and materials

After providing informed consent, participants were seated in a dimly lit room at a distance of approximately 60cm from a 30.5cm x 22.5cm laptop monitor, which was raised to eye level. Participants sat with their index finger positioned ready to respond using a single key on a separate keypad. The keypad was positioned centrally beneath the laptop screen in a fixed position, such that the subject's right hand was centrally aligned with the centre of the image on the screen. The stimuli were presented on the laptop monitor using Presentation® (Neurobehavioral Systems, Inc.) software.

2.1.2.3 Stimuli

Participants observed a series of video clips, consisting of either a human hand executing upwards or downwards movements of the index finger or of a moving object **(Figure 6)**. The object consisted of two parts: a larger stationary rectangle and a smaller square, which moved in either an upward or downward direction.

The stimulus images originated from Poliakoff et al. (2007). To create the hand stimulus, video footage of human right hand was recorded, in which the index finger of the hand executed either upwards or downwards finger movements. In order to allow us to manipulate the time course of movement, this footage was converted into a sequence of still images (digital .avi files – 280 x 224 pixels, approximately 7.5 x 6.5 ° of visual angle), which were presented in quick succession giving the impression of either upward or downward movement of the index finger. To create the object stimulus, a small pink square, which was colour-matched to the fingernail of the hand stimulus, was positioned over the fingernail of the moving finger in each frame, such that the moving square retained the same movement trajectory as the moving finger. A larger stationary rectangle, also colour-matched to the fingernail, was inserted alongside the small moving square to represent the rest of the hand. The moving square and stationary rectangle were purposefully not attached, in order to decrease the likelihood of participants associating the object stimulus with a human hand. The backgrounds of the biological and non-biological stimulus clips were also colour-matched. Both the hand and object stimulus followed a biological motion profile: accelerating towards the middle of the movement, and decelerating towards the end of each movement.

The hand and object stimuli were presented from two different ’viewpoints’: the anatomical view and the mirror view **(Figure 5)**. Mirror view stimuli were created by horizontally flipping the anatomical stimuli.

2.1.2.4 Design and procedure

Participants were informed that they would be observing video clips of either a moving finger or a moving object. They were required to make a pre-specified response of either pressing or releasing a specific key on the keypad, only if a yellow flash go signal suddenly appeared during the movement **(Figure 12)**. At the beginning of each trial, a blank (black) screen was shown for 2000ms to allow participants time to reposition their finger ready to respond to the next trial. The initial start frame consisted of the finger or object in a neutral position presented for 1600ms, which was followed by six movement frames (where the finger or object stimulus moved in either an upwards or downwards direction, viewed from either an anatomical or mirror view) **(Figure 12 and Figure 13)**. Each movement frame was presented for 40ms. A yellow background frame was presented for 80ms, which occurred at one of three variable SOAs, creating the impression of a yellow ‘flash’ during the movement stimulus. The first SOA, referred to as 0ms, occurred directly after the start frame and before the first movement frame **(Figure 12)**, immediately prior to the onset of movement. The second SOA, referred to as 120ms, occurred between the third and fourth movement frames **(Figure 12)**, during the movement. Following the presentation of the six movement frames and yellow flash (at either 0ms or 120ms) the end frame was presented **(Figure 12)**. The third SOA, referred to as 280ms, occurred at movement offset, following the six movement frames and end frame. A second end frame was inserted following the yellow flash go signal to create the impression that the yellow flash occurred during the stimulus movement **(Figure 12)**. The latest SOA (280ms) in the current experiment was equivalent to the earliest SOA used by Gowen et al. (2010, Experiment 2a and 2b). A baseline condition was also included, in which the task relevant go signal (yellow flash) was presented, however no task irrelevant compatible/incompatible movement of the stimulus occurred i.e. the finger/object remained static. To create this condition, the start frame was presented for 1600ms followed by the yellow flash (80ms) followed by the start frame, which was presented again for 40ms. To reduce the possibility of participants pre-programming their response, no-go ‘catch’ trials were included (in which participants were required to withhold response as the yellow flash go signal was not presented during stimulus movement). In addition, ‘jumpy’ oddball trials were interspersed randomly. Oddball trials were created by removing all of the movement frames, leaving only the start frame and end frame. This resulted in a noticeable ‘jump’ in the movement of the stimulus. No yellow flash go signal was presented during oddball trials.

In experiment 1a (control group), participants were asked only to perform the simple reaction time task, in which they were required to respond by pressing or releasing a key on the keypad as quickly as possible when the yellow flash appeared. Participants in this group were not made aware of, or asked to respond to jumpy movements; therefore oddball trials were treated as additional no-go trials.

Participants in experiment 1b (attention-directed group) were given a secondary visual task of observing the stimulus movement and responding verbally (saying the word ‘jump’) when there was an irregular ‘jump’ in the movement (oddball jumpy movement).

Prior to the start of the experiment, participants completed a perceptual task in which 10 example ‘jumpy’ oddball movement trials and ten normal ‘smooth’ movement trials were presented randomly. Participants were required to verbally identify the oddball trials and were required get 100% in this perceptual task to ensure their ability to correctly identify oddball trials.

Participants in both groups completed 16 practice trials (8 go/8 no-go) at the start of the experiment, and 16 practice trials halfway through the experiment when there was a change in response (press/release), giving a total of 32 practice trials throughout the experiment in order for participants to become familiar with the task and required response.

The experiment consisted of a total of 720 trials, which were split into 10 blocks of 72 trials. In blocks 1-5 the participants were required to make either a press key response or a release key response, and their initial response was switched halfway through. In the experimental trials there were 24 experimental conditions: stimulus (2) x view (2) x compatibility (2) x SOA (3). Each of these conditions were presented 20 times (24 x 20 = 480). In addition, the baseline condition (stimulus (2) x view (2) = 4) was presented 20 times (20 x 4 = 80) to give a further 80 further trials. Finally, 80 no-go trials and 80 oddball trials were included in a random order to make a total of 480 + 80 + 80 + 80= 720 trials. All stimulus conditions were presented randomly within each block.

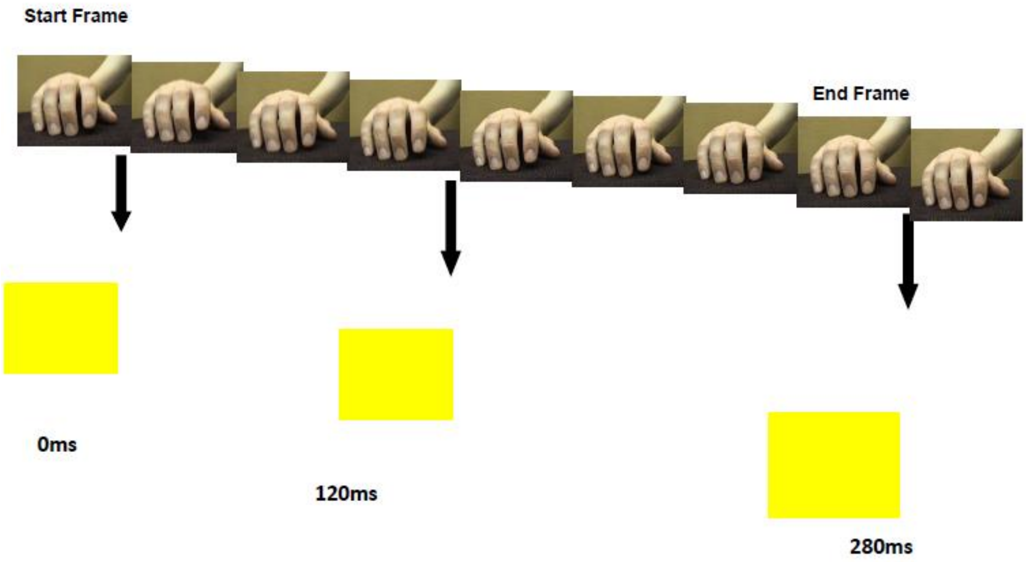

Figure 12: Time course of one experimental trial for the biological (hand) stimulus, depicting a downward finger movement. The trial starts at the left of the image with the initial start frame, where the finger is in a neutral position. This was followed by six movement frames. A yellow response frame was inserted within the movement frame at an SOA of either 0ms, 120ms or 280ms. A second end frame was inserted following the yellow flash at the 280ms SOA only.

Figure 13: Time course of one experimental trial for the non-biological (object) stimulus. This example depicts movement in a downward.

A rest period was given every 72 trials, indicated by a message on the laptop monitor. Halfway through the experiment, prior to the switch of response types, participants were given a longer rest period. During this time, they were required to complete the ELI questionnaire for handedness **(Appendix A1)** and an empathy questionnaire (EQ; Baron-Cohen and Wheelwright, 2004) **(Appendix A2)**. At the end of the experiment, all participants completed an additional questionnaire consisting of six statements and four questions, which aimed to measure how much participants attended to and perceived differences between stimuli during the experiment **(Appendix A4)**. They recorded their answers on a 10-point Likert scale. Statements 1 and 2 examined which stimulus type ‘grabbed the attention’ of the participant more. Statements 3 and 4 examined how well participants attended to and perceived the appearance of the stimuli and the kinematics of the stimulus movements. Statements 5 and 6 asked to what extent participants felt watching the hand and block stimuli affected the movement of their own finger. Questions 7 and 8 asked to what extent participants were aware of which stimulus type they were viewing (the hand or the block). Finally, Questions 9 and 10 asked which stimulus type participants found more ‘interesting’.

2.1.3 Analysis strategy

All statistical analyses were conducted using IBM SPSS Statistics 20.

2.1.3.1 Error data analysis

RTs for trials were excluded from analysis if the participant did not respond or made an incorrect response. RTs were also removed if the response was longer than 1000ms or shorter than 100ms after presentation of the go signal, or if the RT lay outside of 2.173 standard deviations of the participant's mean RT in that condition (Van Selst and Jolicoeur, 1994).

A number of additional errors could be incurred in this task. Anticipation errors refer to when a participant responded before the appearance of the go signal or within 100ms of the go signal. No-go errors refer to responses made on no-go 'catch' trials (i.e. participants responded although no yellow flash go signal was presented). Second response errors refer to instances where a RT had already been produced due to participants erroneously making more than one response for the same trial. Oddball + button error refer to where participants' incorrectly responded with a button press/release response during an oddball trial.

2.1.3.2 Signal detection analysis

In order to measure the performance of participants in experiment 1b in the visual secondary task (monitoring for oddball trials), signal detection analysis was used. Hit rates, false alarm rates, d' measure of sensitivity and C measure of bias were calculated using the following equations:

Hit rate = total verbal response + 0.5/total oddball trials + 1

FA rate = total FAs + 0.5/total correct rejections + 1

d' = z transform of hit rate - z transform of FA rate

C = 0.5 x (z transform of hit rate + z transform of FA rate)

The d' measure of sensitivity measures the sensitivity with which the participants were able to detect the presence of a particular target signal from background events. In this case, we were interested in calculating the sensitivity with which participants were able to detect the oddball movements (target) from normal movements (background events). A high value for d' indicates that the target signal (oddball trials) was readily detected.

The C measure of bias measures the extent to which one response is more probable than another. A negative bias would indicate participants were more likely to incorrectly report the presence of an oddball trial (false alarm) than fail to respond to an oddball trial.

2.1.3.3 Reaction time data analysis

Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects. These comparisons were pre-planned in order to provide an overview of the results.

An initial mixed design repeated measures ANOVA; with response type (press/release) x view (mirror/anatomical) x stimulus (hand/object) x compatibility (compatible/incompatible) x SOA (0, 120, 280) as within-subjects factors, was conducted on participants mean RTs for each experiment. We pre-planned to analyse pressing and releasing responses separately if the overall ANOVA revealed a main effect/interactions with the response type factor, and to average across pressing and releasing responses if not. This initial ANOVA revealed that there was no significant main effect of response type ($F(1,39) = 0.729$, $p = .398$), nor were there any significant interactions with this factor in either experiment 1a or 1b. Mean RTs were therefore averaged across press and release responses and used for further analysis.

Two within-participant ANOVAs were conducted on participants mean RTs (averaged across pressing and releasing responses with view (mirror/anatomical) x stimulus (hand/object) x compatibility (compatible/incompatible) x SOA (0, 120, 280) as within-subjects factors for experiment 1a and experiment 1b. Separate analysis of the two participant groups allowed for a clearer comparison with Gowen et al. (2010), and was required in order to address the separate hypotheses for each experiment.

In addition, conducting paired t-tests between compatible and incompatible RTs at 0ms and RTs for the baseline condition theoretically allows one to determine whether the observed compatibility effects resulted from facilitation from compatible movements, interference from incompatible movements, or a combination of facilitation and interference. The baseline recording (where no movement occurs) can be seen as equivalent to the 0ms SOA, which occurs immediately prior to stimulus movement. In both cases participants are required to respond to task relevant go signal (the yellow flash) which occurs immediately after initial presentation of the stimulus in a neutral position; the only difference being that in the baseline condition, no task irrelevant movement of the stimuli occurs immediately afterwards. However, this comparison was only made in experiments where significant compatibility effects were present at 0ms. While this was not the case in the current experiment, this comparison was made in subsequent experiments in which compatibility effects were present at 0ms.

2.1.3.4 Questionnaire data analysis

Paired t-tests were carried out between questionnaire scores to examine perceived differences between the biological and non-biological stimuli for experiment 1a and 1b.

Maximum compatibility effects were identified for each participant for the finger and object stimuli. Overall ‘difference scores’ between the maximum compatibility effects for the finger and the object were calculated by subtracting each participant's maximum compatibility effect for the object (across all conditions) from their maximum compatibility effect for the finger (across all conditions) for each participant. Maximum compatibility effects were used (as opposed to mean compatibility effects) due to the fact that each individual participant's compatibility effect runs over a slightly different time course, and compatibility effects tend to become negative across SOAs; therefore taking the mean compatibility effect across SOAs is unlikely to provide a good measure of the participant's compatibility effect.

In experiment 1a, we were particularly interested in investigating whether there would be a relationship between: a) participant's empathy scores and their maximum compatibility effects/difference scores; b) participant's empathy scores and self-reported difference scores between the finger and object; c) participant's difference score and their perceived self-reported difference score. Therefore, Pearson's correlation tests were conducted in order to examine whether these relationships were present.

2.1.4 Results

2.1.4.1 Analysis of error data

RTs were excluded based on exclusion criteria detailed in **section 2.1.3.1.** This resulted in an average loss of 2.85% and 2.37% of trials from participants in experiment 1a and 1b respectively. Overall, participants in both groups made a low level of errors **(Table 3 and 4)**; therefore no individual participant's data was removed from the study. The error participants were most prone to was the oddball + button press error, although this was still a relatively low occurrence, occurring in 5.19% of oddball trials on average in experiment 1a (where oddballs were treated as additional no-go trials), and 6.63% of oddball trials on average in experiment 1b. On average, the vast majority (95.5%) of anticipation errors occurred at an SOA of 280ms, suggesting that the anticipation of the yellow flash caused participants to react prior to its appearance.

Table 3: Mean (± SE) number of errors calculated as a percentage of the total number of trials in which the error could occur for experiments 1a, 1b, 2 and 3.

Type of Error (total number of trials where error could occur)	Mean % Error (± SE) Experiment 1a	Mean % Error (± SE) Experiment 1b	Mean % Error (± SE) Experiment 1 (Overall)	Mean % Error (± SE) Experiment 2	Mean % Error (± SE) Experiment 3
Anticipation Error (640)	1.50 (± 0.54)	0.43 (± 0.10)	0.91 (± 0.27)	0.69 (±0.19)	1.17 (± 0.19)
No-go Error (80)	4.5 (± 0.57)	4.44 (± 1.01)	4.47 (± 3.62)	1.94 (± 0.43)	3.59 (± 0.52)
Second response error (640)	1.23 (± 0.18)	0.80 (± 0.08)	1.02 (± 0.10)	0.54 (±0.13)	1.15 (± 0.20)
Oddball trial + button error (80)	5.19 (± 0.83)	6.63 (± 0.87)	5.91 (± 0.60)	-	-
Beep trial + button error (80)	-	-	-	3.97 (±0.46)	-

Table 4: Mean % no-go and anticipation errors (± SE) made by participants in each condition. No-go errors were made out of a potential 80 trials and anticipation errors were made out of a potential 640 trials. **Bold** type represents compatible trials.

	View	**Mean % No-go errors – Expt 1a**	**Mean % No-go errors – Expt 1b**	**Mean % Anticipation errors – Expt 1a**	**Mean % Anticipation errors – Expt 1b**
Finger	Mirror	**0.47 (± 0.09)** 0.25 (± 0.08)	**0.34 (± 0.10)** 0.19 (± 0.06)	**1.72 (± 0.04)** 1.72 (± 0.05)	**0.94 (± 0.03)** 0.63 (± 0.02)
	Anat.	**0.19 (± 0.06)** 0.28 (± 0.08)	**0.25 (± 0.07)** 0.13 (± 0.05)	**2.03 (± 0.04)** 1.56 (± 0.03)	**0.62 (± 0.02)** 0.31 (± 0.01)
Object	Mirror	**0.22 (± 0.09)** 0.01 (± 0.09)	**0.40 (± 0.09)** 0.40 (± 0.09)	**1.72 (± 0.03)** 2.19 (± 0.05)	**0.31 (± 0.01)** 0.31 (± 0.01)
	Anat.	**0.19 (± 0.06)** 0.41 (± 0.10)	**0.22 (± 0.06)** 0.34 (± 0.07)	**2.03 (± 0.05)** 0.94 (± 0.03)	**0.16 (± 0.01)** 0.94 (± 0.03)

2.1.4.2 Performance in attention-directed task

Mean hit rates show that participants' ability to accurately detect oddball trials was high, which was expected due to the obvious design of the oddball trials. All participants detected between 89 - 99% of the oddball trials on average; the overall mean hit rate being 0.98 (98%). In addition participants had a very low false alarm rate (0.02) suggesting it was uncommon for participants to incorrectly report the presence of an oddball trial during a normal movement trial.

A one sample t-test revealed that the mean d' (4.99) (SD = 0.29) was significantly greater than 0 (*t*(19) = 77.368, *p* = .000), indicating that recognition of oddballs was above that of chance, and that participants had no difficulty detecting oddball trials.

The positive mean value for bias (C) (M = 0.44; SD = 0.11) indicates that participants were more likely to fail to respond to an oddball trial than to incorrectly report the presence of an oddball trial.

2.1.4.3 Analysis of reaction time data

Overall mean RTs (ms) (± SE) are presented in **Table 5**. Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to determine the presence or absence of significant compatibility effects. Statistically significant results are indicated by asterisks in **Table 5**. In experiment 1a, there was a significant compatibility effect for the finger stimulus at 120ms in the anatomical view. In experiment 1b, there was a significant compatibility for the object stimulus at 120ms in the anatomical view.

A paired t-test between the average RTs of participants in experiment 1a and experiment 1b group revealed that the average RT was significantly faster in experiment 1a (M = 323.51ms) compared to experiment 1b (M = 381.71ms) (*t*(19) = -2.536, *p* = .020). The slower RTs in experiment 1b can be explained by the secondary oddball detection task demanding additional cognitive resources.

Table 5: Mean RTs (ms) (± SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (*p* < .05).

Stimulus	View	SOA (ms)	Mean RT in non attention-directed group (ms) (± SE)	Mean RT in attention-directed group (ms) (± SE)
Finger	Mirror	0	**355.08 (± 19.16)** 360.82 (± 19.79)	**412.36 (± 13.42)** 422.97 (± 15.34)
		120	**307.64 (± 16.15)** 307.96 (± 17.06)	**357.54 (± 13.12)** 366.01 (±13.62)**p=.072*
		280	**299.60 (± 14.83)** 306.66 (± 14.95)	**359.43 (± 12.89)** 365.94 (± 10.49)
	Anatomical	0	**356.75 (± 19.67)** 352.98 (± 17.82)	**423.84 (± 15.93)** 419.53 (± 14.22)
		120	**294.68 (± 14.84)** 306.98 (± 17.16)*	**362.77 (± 14.07)** 366.13 (± 12.10)
		280	**301.91 (± 13.62)** 306.89 (± 16.66)	**362.41 (± 10.32)** 364.61 (± 10.69)
Object	Mirror	0	**372.39 (± 19.35)** 362.22 (± 18.00)	**424.07 (± 13.00)** 428.35 (± 12.92)
		120	**311.18 (± 15.91)** 306.49 (± 17.43)	**369.05 (± 10.78)** 361.42 (± 12.51)
		280	**303.10 (± 14.50)** 302.68 (± 15.18)	**351.45 (± 11.03)** 354.88 (± 10.65)
	Anatomical	0	**363.43 (± 18.73)** 365.87 (± 18.63)	**424.09 (± 14.32)** 427.14 (± 13.97)
		120	**307.57 (± 16.02)** 306.76 (± 16.83)	**353.81 (± 12.04)** 371.53 (± 14.32)*
		280	**302.76 (± 15.52)** 301.99 (± 15.86)	**359.18 (± 12.63)** 355.31 (± 11.53)

2.1.4.3.1 Experiment 1a

In the control group, there was a significant interaction between compatibility and stimulus (*F*(1,19) = 6.580, *p* = .019) **(Figure 14)** indicating that mean compatibility effect for the finger stimulus (M = 4.44ms) was significantly greater than compatibility effect the object stimulus (M = -2.40) (*t*(19) = 2.794, *p* = .012) across all three SOAs. The interaction between stimulus, compatibility and SOA did not reach statistical significance (*F*(2,38) = .682, *p* = .512)

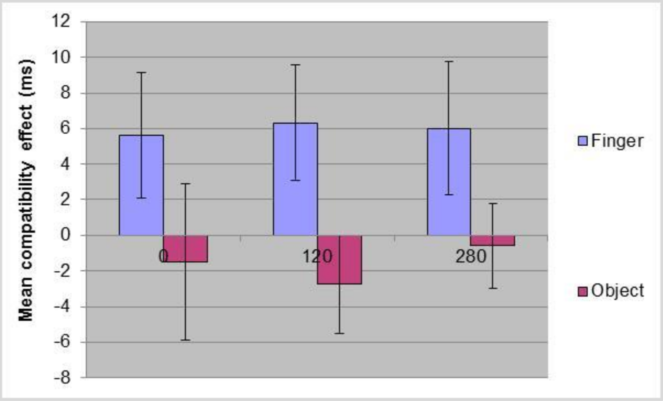

Figure 14: Mean compatibility effects across SOAs in experiment 1a.

Paired t-tests comparing compatible and incompatible RTs at 0ms SOA and baseline RTs at 0ms were not carried out due to the fact no significant compatibility effects were present at 0ms, which emerged later at 120ms for the finger (anatomical view) in experiment 1a **(Table 5)**.

2.1.4.3.2 Experiment 1b

In the attention-directed group, there was a significant interaction between view, stimulus and compatibility (*F*(2,38) = 4.512, *p* = .047) **(Figure 15a and 15b)** indicating that compatibility effects were significantly stronger for the finger stimulus (M = 9.41ms) compared to the object stimulus (M = .025) in the mirror view (*t*(19) = 2.312, *p* = .032). There was no difference between compatibility effects for the finger and object in the anatomical view (*t*(19) = -.778, *p* = .446); nor were there any differences between compatibility effects for the finger or the object stimulus between the mirror and anatomical views.

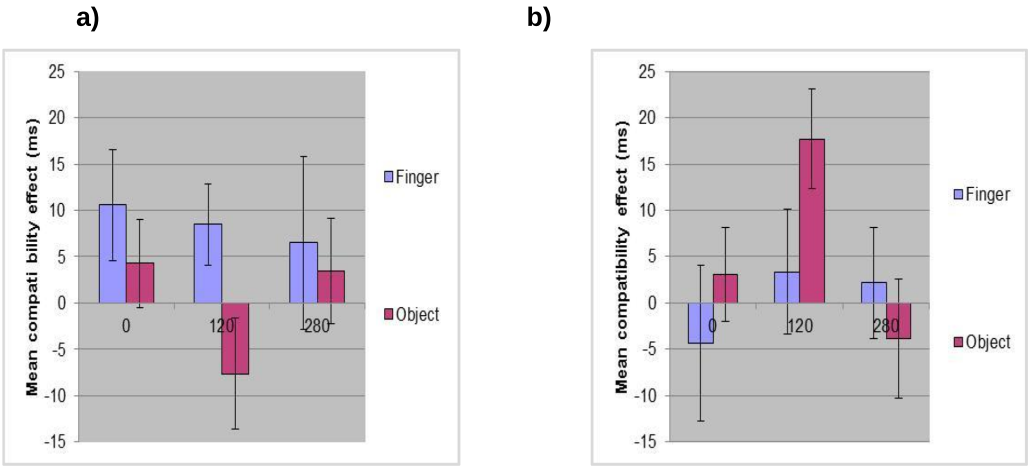
a) b)

Figure 15: a) Mean compatibility effects for finger and object stimulus at each SOA in the mirror view; **b)** Mean compatibility effects for the finger and object stimulus at each SOA in the anatomical view.

There was an interaction between view, compatibility and SOA (*F*(2,38) = 3.232, *p* = .051), which was bordering on significance, indicating that mean compatibility effects were greater when viewed from the anatomical view (M = 10.54ms) compared to the mirror view (M = 0.41ms) an SOA of 120ms (*t*(19) = -2.503, *p* =.058). The difference between compatibility effects between the mirror and anatomical views was not significant at the 0ms or 280ms SOAs (*p* >.126). In the anatomical view, compatibility effects were significantly stronger at 120ms (M = 10.54ms) compared to 280ms (M = -.84). In addition compatibility effects were stronger at 120ms (M = 10.54ms) compared to 0ms (M = -.63ms) and this difference was approaching significance (*t*(19) = -2.016, *p* = .058). However, in the mirror view there was no significant difference between compatibility effects between the different the SOAs (*p* > .196). These differences appear to be driven by the object condition, where there is a significant compatibility effect for the object at 120ms in the anatomical view

(Table 5, Figure 15); however the interaction between view, stimulus, compatibility and SOA did not reach significance (*F*(2,38) = 1.244, *p* = .300).

Paired t-tests comparing compatible and incompatible RTs at 0ms SOA with the baseline RTs at 0ms were not carried out due to the fact no significant compatibility effects were present at 0ms for either stimulus, which emerged later at 120ms (anatomical view) for the object stimulus in experiment 1b **(Table 5)**.

2.1.4.4 Analysis of questionnaire data

Mean questionnaire scores for each group and overall are displayed in **Table 6.**

Table 6: Mean questionnaire scores for experiments 1a, 1b, 2 and 3. In response to statement 1-6: a score of 10 represents 'agree'; 5 represents 'neither agree nor disagree' and 0 represents disagree. In response to questions 7-10: a score of 10 represents 'very much'; a score of 5 represents 'to some extent' and a score of 0 represents 'not at all'.

No.	**Question/Statement**	**Experiment**					
		1a	**1b**	**2**	**3 (Finger First)**	**3 (Object first)**	**3 (mean)**
1	Watching the finger grabbed my attention more than watching the object	6.8	5.2	6.1	6.8	7.5	7.2
2	Watching the object grabbed my attention more than watching the finger	3.3	4.8	3.7	4.1	3.8	3.9
3	The clips of the object and the finger were similar in terms of movement	5.6	5.2	6.6	6.8	7.5	7.2
4	The clips of the object and the finger were similar in terms of appearance	2.9	2.7	2.5	3.1	3.4	3.3
5	Seeing the object move made me want to move my own finger	2.2	3.2	2.9	4.6	3.9	4.8
6	Seeing the finger move made me want to move my own finger	5.8	4.8	6.3	7.8	8.3	8
7	When watching each video clip, how much were you aware that you were seeing either the hand or the object?	8.6	7.0	7.9	6.4	8.1	7.2
8	When the video clips changed between the object and the hand how much did you notice his change?	8.0	6.9	8.3	7.4	8.8	8.1
9	To what extent, if at all, was watching the object move more interesting than watching the finger?	4.5	3.8	3.9	3.9	4.2	4.1
10	To what extent, if it all, was watching the finger move more interesting than watching the object move?	3.7	5.3	5.3	5.1	5.8	5.5

Interestingly, questionnaire responses of both participant groups were generally in line with their RT responses. For example, participants in experiment 1a indicated that the finger was significantly more attention grabbing (M = 6.8) than the object (M = 3.3) (*t*(19)= 4.080, *p* = .001). This mirrors the fact that imitative compatibility was present for the hand stimulus and not the object stimulus. However, the mean score for participants in experiment 1b were close to neutral and did not differ between hand (M = 5.2) and object (M = 4.8) (*t*(19) = 0.264, *p* = .795), suggesting participants felt neither of the stimuli were more attention grabbing than the other. This was reflected in participants RT data, in that the compatibility effect for the finger and the overall human bias was removed (being present only in the mirror view, which is more likely to be contaminated with spatial compatibility effects). Furthermore, there was a significant difference between responses for question 2 in experiment 1a (M = 3.3) and 1b (M = 4.8), mirroring a bias for the hand in the control group and a lack of bias between the stimuli in the attention-directed group (*t*(19) = -2.448, *p* =.024). Similarly, the difference between responses for question 1 were approaching significance between experiment 1a (M = 6.8) and experiment 1b (M = 5.2) (*t*(19) = 1.932, *p* = .068).

For statement 3, participants responded neutrally with regards to the similarity between the movement of the finger and the object and there was no significant difference between scores between the two groups (*t*(19) = .434, *p* = .669). There was no significant difference between their scores for question 4 (*t*(19) = .786, *p* = .442); both groups perceived the finger and block as very different in appearance.

Questions 7 and 8 both asked to what extent participants were aware of the differences/noticed the changes between the two stimuli therefore scores were averaged across the two questions. There was a significant difference between scores for experiment 1a and 1b (*t*(19) = -2.232, *p* = .038); participants in experiment 1a scored this question highly (M = 8.4), however the participants in experiment 1b scored the question relatively more neutrally (M = 6.9).

Finally, in response to questions 9 and 10, scores were close to neutral indicating participants did not find either stimulus more ‘interesting’ than the other.

2.1.4.4.1 Relationship between EQ and maximum compatibility effects

Mean empathy scores for the control group (experiment 1a) were slightly lower (M = 40.55) then in the attention-directed group (experiment 1b) (M = 45), however a paired t-test revealed that there was no significant difference between empathy scores (*t*(19) = -1.142, *p* = .268). Due to the unexpected compatibility effect results in experiment 1b, the relationship between the EQ/self-reported attention questionnaire and difference scores was analysed for experiment 1a only.

In experiment 1a there was a significant negative correlation between participant’s maximum compatibility effects for the object and EQ scores, suggesting that participants who reported to being less empathetic had higher compatibility effects for the object (*r*(20) = -.454, *p* = .044) **(Figure 16)**. The correlation between maximum compatibility effects for the finger and EQ scores was not significant (*r*(20)= -.286, *p* = .221).

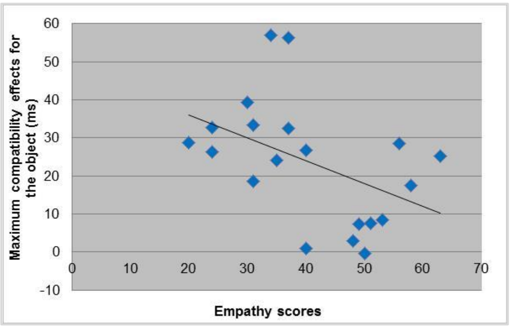

Figure 16: Negative correlation between maximum compatibility effects for the object and EQ scores.

2.1.4.4.2 Relationship between EQ and difference scores

Difference scores were calculated as described in **Section 2.1.3.4**. There was no correlation between difference scores and EQ scores in experiment 1a (*r*(20) = .181, *p* = .445).

2.1.4.4.3 Relationship between difference scores and self-reported attention questionnaire scores

In experiment 1a the negative correlation between statement 1 'watching the finger grabbed my attention more than watching the object' and difference scores was approaching significance, indicating participants who disagreed with the statement had higher difference scores (*r*(20) = -.430, *p* = .059) **(Figure 17)**. However this correlation does not make sense and appears to be driven by four participants who gave lower (between 2-4) scores in answer to this statement yet had a higher difference scores. However, all the other participants scored between 6-10. When these four participants are removed from analysis, this correlation disappears, indicating that this is not an overall trend in this group of participants (*r*(16) = -.120, *p* = .658).

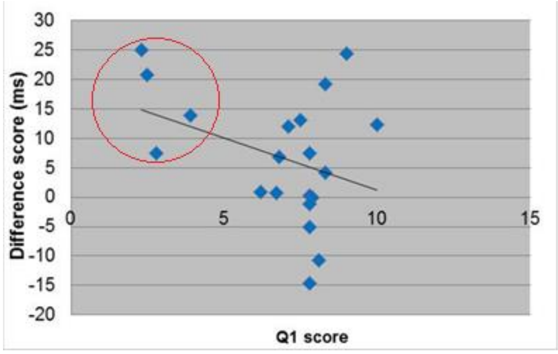

Figure 17: Negative correlation between difference scores and scores for statement 1: 'Watching the finger grabbed my attention more than watching the object' was approaching significance; however when four participants (circled in red) were removed from analysis the correlation was not present.

2.1.4.4.4 Relationship between EQ and self-reported attention questionnaire scores

Pearson’s correlation tests were conducted between participant’s EQ scores and participant’s questionnaire answers for both groups.

In experiment 1a, there was a significant negative correlation between scores for statement 5 ‘seeing the object move made me want to move my own finger’ and EQ scores (*r*(20) = -.465, *p* = .039), indicating that participants who reported to being more empathetic tended to report that seeing the object move made did not make them want to move their own finger, whereas participants who reported to being less empathetic reported that seeing the object move did make them want to move their own finger **(Figure 18)**.

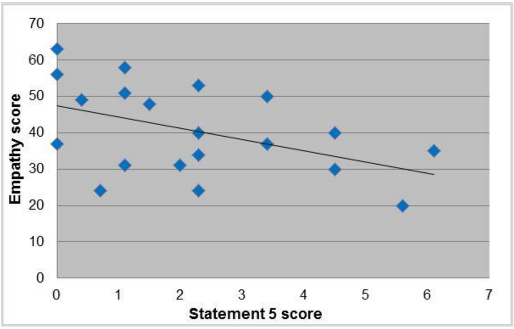

Figure 18: Negative correlation between EQ scores and scores for statement 5: ‘Seeing the object move made me want to move my own finger’.

Similarly, there was a significant negative correlation between scores for question 9 and EQ scores (*r*(20) = -.525, *p* = .018), indicating that participants who reported to being less empathetic tended to find the object more interesting than the finger, whereas the participants who reported to being more empathetic did not **(Figure 19)**.

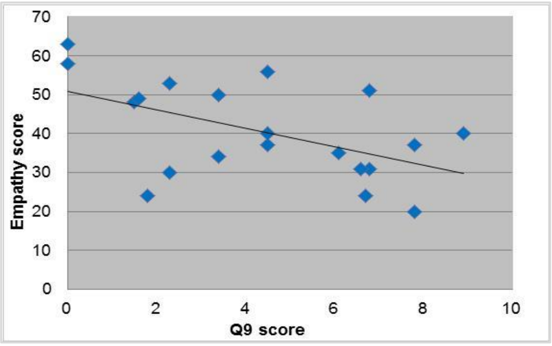

Figure 19: Negative correlation between EQ scores and scores for statement 9: ‘To what extent, if at all, was watching the object move more interesting than watching the finger?’.

In experiment 1b, there was a significant positive correlation between scores for statement 5 and EQ scores (*r*(20) = .537, *p* = .015), indicating that participants who reported to being less empathetic tended to report that seeing the object move did not make them want to move their own finger, whereas participants who reported to being more empathetic reported that seeing the object move did make them want to move their own finger **(Figure 20)**.

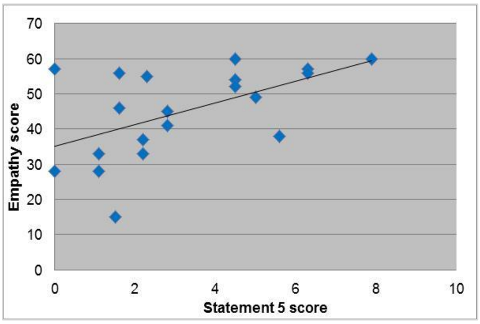

Figure 20: Positive correlation between empathy scores and scores for statement 5: 'Seeing the object move made me want to move my own finger'.

There was also a significant positive correlation between scores for statement 6 and EQ scores (*r*(20) = .523, *p* = .018), indicating participants who reported to being less empathetic tended to report that seeing the finger move did not make them want to move their own finger, whereas more empathetic participants reported that seeing the finger did make them want to move their own finger **(Figure 21)**.

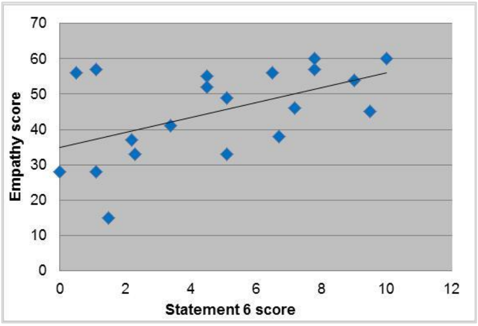

Figure 21: Positive correlation between empathy scores and scores for statement 6: 'Seeing the finger move made me want to move my own finger'.

Finally, there was a significant positive correlation between scores for question 7 and EQ scores (*r*(20) = .498, *p* = .025), indicating that who reported to being less empathetic tended to report that they were less aware of the fact they were viewing either a hand or an object whereas participants with a higher empathy score reported that they were more aware of this fact **(Figure 22)**.

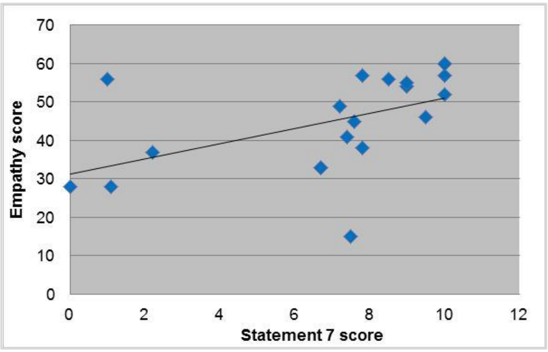

Figure 22: Positive correlation between empathy scores and scores for question 7: "When the video clips changed between the object and the hand how much did you notice his change?".

2.1.5 Discussion

In experiment 1a, we have successfully reinstated the 'human bias', replicating previous findings of enhanced imitative compatibility effects for biological stimuli relative to non-biological stimulus. These findings confirm that, as hypothesized, imitative compatibility effects can be produced when a diffuse go signal presented at earlier SOAs when greater attention is focused on stimulus movement (as opposed to post stimulus movement). However, experiment 1b revealed that the secondary oddball detection task was not successful in directing attention to the movement. Moreover, completing this secondary task created dual task interference, leading to the consequent removal of the previously observed imitative compatibility effect for the finger stimulus. In addition, we have found a relationship between: a) empathy and maximum compatibility effects for the object stimulus (but not maximum compatibility effects for the finger stimulus or difference scores); b) difference scores and self-reported differences questionnaire c) empathy and self-reported differences questionnaire; however, there was no apparent relationship between self-reported questionnaire scores and difference scores. These findings will now be discussed in turn.

2.1.5.1 Experiment 1a

We predicted that compatibility effects for the finger stimulus would be stronger relative to the object stimulus when using earlier SOAs and this prediction was confirmed. These results replicate a number of behavioural studies which have reported stronger imitative compatibility effects for observation of biological relative to non-biological stimuli movements (Brass et al., 2001a; Gowen et al., 2010; Kilner et al., 2003; Press et al., 2005), supporting the idea that the human MNS is tuned to represent biological motion to a greater extent than non-biological motion.

The significant interaction present between stimulus and compatibility shows that the observation of the finger moving primed participants' own finger movements, whereas the observation of the object moving did not. The fact that significantly stronger compatibility effects were produced for the finger stimulus relative to the object in experiment 1a is a significant finding. This is because Gowen et al. (2010, Experiment 2a) used a similar methodology, differing from experiment 1a only in the fact that post-stimulus durations were used; however, they found that compatibility effects for the finger and object stimuli were not significantly different. As discussed previously, the authors suggested that the absence of a typical biological bias could be explained by the use of a diffuse flash go signal, which may have created a more diffuse spread of attention, causing less attention to be drawn to stimulus differences. In contrast, when Gowen et al. (2010, Experiment 1), used a localised cross go signal appearing on the moving part of the stimulus, this may have focused participants attention on stimulus movement leading to the presence of a human bias. In the current study when the diffuse flash go signal occurred during stimulus movement at various SOAs, a significant difference between imitative compatibility effects for the finger and the object was produced.

One possible explanation for the current findings is differences in the attentional strategy employed by participants due to the different SOAs used. In Gowen et al. (2010) the yellow flash go signal appeared after the stimulus movement had occurred in every trial. Therefore, it is plausible that participants may have failed to attend to the stimuli (i.e. ‘zoned out’ of the movement of the stimuli completely) due to the fact participants likely discerned that the go signal was always presented after the stimulus movement. In addition, it is likely that the diffuse yellow flash used would have created a more diffuse spread of attention. However, in the current experiment, the yellow flash occurred during stimulus movement, when participants were more likely to be attending to the movement of the stimuli, thus the human bias was reinstated. The use of a diffuse go signal allows one to investigate the time course of imitative compatibility effects, whilst removing lateral spatial compatibility (from using a localised go signal appearing on the stimulus) and stimulus saliency confounds (from using movement onset as a go signal). However, these results suggest imitative compatibility effects are only present when a diffuse go signal is presented at movement during stimulus movement, when greater attention is focused on the stimulus.

This finding is at odds with studies that have observed differential imitative compatibility effects between biological and non-biological stimuli at post-stimulus durations (Poliakoff et al., 2007; Gowen et al., 2010, Experiment 1). A plausible explanation for these conflicting findings is the fact that such studies have used an ‘X’ cross go signal that appeared on the stimuli. A localised cross go signal would draw attention towards the stimuli, causing a biological bias to be present. On the other hand a diffuse go signal does not require attention to the stimulus. This suggests that the use of the diffuse flash widening participants spread of attention, in combination with presentation at movement offset (allowing participants to zone out of the movement) was responsible for the absence of imitative compatibility effects in Gowen et al., 2010 (Experiment 2a and 2b). However, as greater attention is focused on stimulus movement at early SOAs, the human bias of imitative compatibility effects was reinstated in the current experiment. This suggests that the emergence of imitative compatibility effects depends on: 1) whether the go signal used focuses attention on stimulus movement, or draws attention away from stimulus movement, and; 2) when the go signal is presented during stimulus movement (when attention is greater) or after stimulus movement (when attention is reduced or absent). These results strongly suggest that imitative compatibility effects do not occur ‘automatically’ but are modulated by attentional processes.

A relevant study by Biermann-Ruben et al. (2008) used a modified effector compatibility RT task. In this task participants were required to lift either the index or little finger when either a high or low pitched auditory tone was presented, either at movement onset or at movement offset. The pitch of the tone coded which finger the subjects had to lift: half of the participants were instructed to lift the index finger to the low tone and the little finger to the high tone, and the other half were given the opposite instruction. Participants observed irrelevant upwards and downwards movements of a finger (biological condition) or red dot moving upwards or downwards over the static finger (non-biological condition). The results are difficult to interpret because two components of compatibility were looked at simultaneously - movement compatibility as the stimuli moved both upwards and downwards- and effector (index or little finger). However, when movement direction was compatible they found a stronger effector compatibility effect for the biological stimuli compared to non-biological stimuli at the onset of movement, whereas at the offset of movement effector compatibility effects for biological and non-biological stimuli did not differ. Based on these results Biermann-Ruben et al. suggested that the facilitatory effect of observing biological motion is transient and requires a close temporal relationship between the observed and executed movement, thus imitative compatibility effects might only be present if the task requires an immediate response, while visual processing is taking place.

However, based on the assumption that the auditory tone used in Biermann-Ruben study is equivalent to the diffuse flash (in that neither demand attention to the stimulus), a similar attentional hypothesis could provide an alternative explanation as to why they only found a human bias at movement onset and not at movement onset. Furthermore, our interpretation suggests that if they had used a go signal which drew attention to the stimulus (as opposed to a diffuse auditory go signal), the human of imitative compatibility may have been present in the offset condition. Interestingly, in Bierrmann-Ruben experiment participants were required to fixate on a central located white cross (positioned on the horizontal midline of the stimulus with equal distance to the tip of the index and little finger) throughout the experiment during stimulus, however despite the fact they were asked to fixate on an area in close proximity to stimulus movement, a human bias was only present during the onset condition. The fact that this effect was present only in the onset condition could suggest that only the sudden onset of movement captured their attention. Participants may have then re-focused on the fixation cross, zoning out of the movement towards the end of the movement. In addition, since initial visual processing and recognition of the stimulus and its biological origin occurs rapidly, this might also explain these results.

In agreement with their findings, in the current study we have found that imitative compatibility effects and a biological were only present in at earlier SOAs using a diffuse go signal. However, this may only be relevant in situations where a go signal which creates a diffuse spread of attention is used. Our findings suggest that rather than a specific temporal window during which imitative compatibility effects emerge (i.e. early onset during stimulus movement), based on the fact imitation is present at post stimulus movement durations when attention is drawn to stimulus movement (Gowen et al., 2010), that the emergence of imitative compatibility effects may be dependent on attention.

Encouragingly, in the current experiment a significant compatibility effect for the finger at 120ms SOA were observed in the anatomical view (where spatial compatibility should be removed) and there was no overall influence of view suggesting that compatibility effect is likely to be based on true imitative compatibility rather than spatial compatibility effects.

2.1.5.2 Experiment 1b

The 'oddball' detection secondary task was designed to draw attention towards the movement of both stimuli. We predicted that this would either lead to a larger difference in imitative compatibility effects for the finger or the block if attention was further drawn towards the differences in the stimuli, or more equal imitative compatibility effects if the manipulation caused attention to be drawn to both stimuli equally. However, no significant compatibility effects for the finger stimulus were present in any individual condition in experiment 1b, suggesting that concurrently monitoring for oddball trials removed the imitative compatibility effect for the finger stimulus (anatomical view), previously observed in experiment 1a. This suggests that despite being extremely noticeable, the use of the secondary task of monitoring for oddballs still interfered with the primary imitation task. This replicates the findings of Gowen et al. (2010, Experiment 2b), who also used (more difficult) oddball trials as the attentional manipulation, resulting in a loss of significant compatibility effects. They suggested that the secondary task of identifying the subtle oddball trials was too difficult or attentionally demanding, shown by the fact that sensitivity scores for the detection of oddball trials were low (d'= 1.99). However, the current experiment has demonstrated that even when the oddball trials were extremely easy to spot (d'= 4.99) with participants correctly identifying 98% of the oddball trials on average, significant compatibility effects were still not produced. This suggests that perhaps the use of a secondary visual task, regardless of difficulty, reduces imitative compatibility effects.

The fact that RTs were significantly slower in the attention-directed group, and imitative compatibility was removed provides evidence that the secondary task caused dual task interference. The idea that, at any given time, the human information processing system can only process a limited amount of information, and use this information to generate behaviour without interference has been a topic of interest to psychologists for many years. It is well known that we have attentional limits that influence performance when we perform more than one activity at the same time, and dual-task paradigms have been most commonly used by researchers to understand such attentional limitations.

Three main theoretical concepts have been proposed regarding how and why attentional limitations arise in dual task situations (see Pashler, 1998 for a review). The first concept is that of a processing 'bottleneck'. The assumption in this approach is that, since the human information processing system performs one task at a time in a serial order, a bottleneck would arise when, in a dual task situation, two tasks require the same mental mechanism at the same point in time. At this point, only a limited amount of information would be selected for further processing and the remaining information would be 'filtered out'. If this explanation is correct, there are a number of possible interpretations. For example, it could be that the brain only has a single mechanism for performing the mechanism in question, or alternatively, that the mechanism in question is performed by different neural machinery that inhibit one another such that only one or the other may be carried out at the same time. Such a bottleneck might depend on the information being processed or the type of mental operation to be carried out. Based on this theory, it is possible that the imitation (action observation) task and the oddball detection required the same mental process at the same point in time. Given that both imitative compatibility and the oddball task were visual in nature, it is likely that they used similar mental processes, adding weight to this interpretation. In addition, the oddball task may have been prioritised because the participants were explicitly asked to carry out the oddball detection task; however the production of the imitative compatibility effect occurs without conscious awareness.

This also fits in well with the second concept, which suggests that attentional limitations are the result of 'crosstalk' which is directly dependant on the content of the information being processed. This theory predicts that dual task interference depends on the similarity of the mental representations involved in the task (Navon and Miller, 1987). A number of researchers have investigated how task similarity limits dual task performance and have found that tasks interfere with one another if they have the same stimulus modality (e.g. both visual/both auditory tasks), make use of the same stages of processing (e.g. visual input, internal processing, response) or rely on related memory codes (Pashler, 1994). Task difficulty has been shown to be a limiting factor in dual task performance (Gopher, 1980). In addition, practise has been shown to improve dual task performance. This improvement could occur either through the adoption of more effective strategies to minimize dual task interference, or by reducing demand on attentional resources by shifting from controlled processing mechanisms to more automatic (efficient) processing (Schneider and Shiffrin, 1977). A key characteristic of automatic processing is that it places minimal demands on attentional resources. With the idea of 'automatic processing' in mind, it is interesting that despite the fact that the current results suggest participants found the oddball detection task easy, this task still interfered with the imitation task. This supports the idea that so-called 'automatic' imitation task is actually a more controlled process than previously thought, as if it were an automatic process we would not expect the easy secondary task to have created dual task interference.

The third concept, known as the ‘capacity sharing model’, has gained the most popularity. This account posits there may be one (central capacity sharing model; e.g. Norman and Shallice (1986) or more (multiple capacity mode e.g. Allport, 1989; Wickens, 1980) ‘pools’ of processing resources that can be divided among different tasks in a graded fashion. According to this theory, processing of two different tasks can occur in parallel, however the speed and efficiency of the processing depends on the total capacity available to the task. According to this model, when the cognitive resources required to perform two tasks simultaneously exceed the total capacity of the system, resources allocated to one or both of the tasks is reduced, leading to a decrease in performance. Prioritisation of one task increases the resources allocated to that task, minimising the deterioration of performance, however, this comes at the cost of reduced allocation of resources and greater dual task interference in the non-prioritised task. Based on this model it is possible that in experiment 1b, rather than attention enhancing imitation, because the imitation task and the secondary visual task were completed simultaneously there was competition for cognitive resources. In this case, the secondary oddball detection task was prioritised, leading to the removal of imitative compatibility effects for the finger stimulus. The central capacity-sharing model predicts less dual task interference when two tasks access different sensory modalities, as each modality is entitled to its own separate attentional resource. If two or more tasks are similar they will draw on a common resource pool, thus affecting performance negatively. Conversely if the tasks require separate resources then performing both at the same time can occur with minimal interference.

Therefore, an interesting question arising from the removal of imitation for the finger in experiment 1b, is whether or not this due to general cognitive load of having a secondary task to perform; or whether this was due to the fact the imitation task and the oddball detection task were both drawing on the same sensory modality (visual). For example, it is possible that if the secondary task drew on a different sensory modality, such as a secondary auditory task, that imitation would be present. Consistent with this idea, a recent study has found dual task interference with movement observation with a secondary visual, but not auditory, task (Saucedo Marquez et al., 2011). When subjects observed actors lifting objects of different weights, and measured corticomotor excitability of the muscles involved in the observed actions whilst TMS was applied, weight related modulation of M1 excitability was absent with a secondary visual task. In their study, the secondary visual task involved detecting the colour change of the rim surrounding the observed movement, thus changing rim colours may have acted as visual distractors. However, in experiment 1b we attempted to draw attention towards the stimulus. Therefore, our results agree with and extend their findings, in that even when the visual task relies on the participant paying attention to the observed movement, a secondary visual task still interferes with movement observation, leading to the loss of imitation effects in experiment 1b. In addition, they found that no dual task interference was present when using a secondary auditory task (see **Section 1.3** for description methodology regarding of TMS evoked MEPs and **Section 2.2** where Saudeco

Marquez et al. (2011) study is described in further detail). Previous cross-modal dual task interference studies have indeed observed this to be true. For example, Alais et al. (2006) examined the cost of dividing attention across visual and auditory modalities, compared with dividing attention between two tasks in the same sensory modality. They found that visual contrast discrimination thresholds were unaffected by concurrent chord or pitch discrimination tasks, and thresholds for pitch/chord discrimination were virtually unaffected by concurrent visual search or contrast discrimination tasks. This further supports the idea that the absence of imitative compatibility effects in experiment 1b may be due to the fact that two visual tasks were used. This idea will be explored further in **experiment 2**.

An interaction between view, stimulus and compatibility was present in experiment 1b, indicating that compatibility effects were significantly stronger for the finger stimulus compared to the object stimulus in the mirror view (however it should be noted that as discussed, there were no significant compatibility effects for the finger stimulus in any individual condition in this group). The fact that this effect is only present in the mirror view (and not across both views as in experiment 1a) suggests that the oddball manipulation directed attention toward the spatial aspect of the movement, increasing imitation for finger stimulus in the mirror view (where imitative compatibility effects are likely to be contaminated with lateral spatial compatibility); but removing imitation for the finger in the anatomical view (likely to reflect imitative compatibility) due to dual task demands. This is in line with the findings of Gowen et al. (2010, Experiment 2b) who found that although significant compatibility effects were not produced in any individual condition, imitative compatibility effects for the mirror view were significantly greater than for the anatomical view. This suggests lateral spatial compatibility effect in this paradigm is a robust effect, being present even when dual task interference is present. This consistent advantage for the mirror view emphasizes the importance of controlling for lateral spatial compatibility in future experiments. One way of controlling for this would be to make the participant’s response movement spatially separate from the observed movement, an idea that has been explored in **Chapter 3**.

A significant compatibility effect for the object stimulus (anatomical view) was present in experiment 1b. This is difficult to explain as there is seemingly no reason why a compatibility effect would be present for the object stimulus but would be removed for the finger stimulus. One possibility is that cognitive resources normally used for inhibiting object imitation (causing the usual human bias observed in experiment 1a) were being occupied by the secondary oddball detection task, which may have additionally caused attention to be drawn to the spatial element. A reduction in control of imitative compatibility effects due to dual task demands could explain why there is possibly a ‘disinhibition’ of imitation for the object at 120ms; and a lack of overall difference in imitation between the finger and object (but a difference for the mirror view due to increased attention to the spatial aspect). However, the removal of imitative compatibility for the finger stimulus and the removal of the overall difference between compatibility effects between the biological and non-biological stimuli supports the idea that the secondary visual task caused overall dual task interference.

2.1.5.3 Questionnaire and empathy findings

It is interesting to note that the between group patterns of responding to the self-report questions and statements generally appeared to be in line with their RT results. For example, questionnaire scores for participants in experiment 1a indicated that they felt that the finger was more attention grabbing and made them want to move their finger more than the object, and this was reflected in the fact that imitative compatibility effects were present only for the finger stimulus. However, the mean score for the attention-directed group were close to neutral for both the finger and the object suggesting that they felt neither stimulus was more attention grabbing than the other, which was reflected by the lack of difference in imitative compatibility effects between the two stimuli. As there was no significant difference in empathy scores between groups it is unlikely that these differences reflect chance differences in personality between participant groups and is therefore more likely to reflect the differences in the attentional manipulation. In addition, participants in experiment 1a gave a mean score of 8.4 for the questions addressing to what extent participants were aware of the differences/noticed the changes between the two stimuli; however participants in experiment 1b scored the question more neutrally (M = 6.95). If the attentional manipulation had worked to draw the attention towards the stimuli in experiment 1b we would have expected them to rate this more highly than participants in experiment 1a. The more neutral score given supports the idea that the oddball manipulation conversely reduced their attention to the stimuli, leading to the absence of imitative compatibility effects observed in this group.

In addition, we found there was a relationship between: a) empathy and maximum compatibility effects for the object (but not maximum compatibility effects for the finger or difference scores); b) empathy and self-reported questionnaire scores; however, there was no apparent relationship between self-reported questionnaire scores and difference scores. These findings will now be discussed in turn.

The fact that there is a relationship between maximum compatibility effects for the object and EQ scores (indicating participants with low empathy scores had a higher maximum compatibility effect for the object) is interesting. In line with this, participants who reported to being less empathetic tended to agree that the object ‘more interesting’ than the finger, whereas more empathetic participants disagreed with this statement. In addition, participants who reported to being more empathetic tended to report that seeing the object move made them want to move their own finger, whereas participants with higher EQ scores tended to disagree with this statement. This in combination with the self-report correlations can be taken to suggest that participants with lower empathy scores may have been more ‘interested in’ and drawn to the object stimulus relative to the finger stimulus. It is therefore possible that enhanced biological motion perception may be reduced in less empathetic individuals due to a lack of interest in human/social stimuli. This may result in either increased imitation for the object stimulus (due to increased attention), or a decreased level of inhibition of processing of the object stimulus in those with lower empathy scores. However, if this explanation were correct then we might have expected to also see a positive correlation for imitative compatibility effects for the finger/difference scores, and it is difficult to interpret why this is the case.

A number of previous studies have found positive correlations between questionnaire measures of empathy and spontaneous mimicry of human stimuli (Harrison et al., 2010; Sonnby–Borgström, 2002), however, these studies involved mimicry of emotional facial expressions, where it could be argued that the relationship between empathy and mimicry could be due to differences in participants' conscious interpretation of the emotions portrayed by the facial stimuli.

A recent study by Haffey et al. (2013) suggests that self-reported empathy (as measured by the EQ) and autistic traits (as measured by the autism quotient questionnaire) modulate the effects of reward on mimicry of social human and robotic hand stimuli. In this study, participants completed a conditioned learning task in which participants participated in a card game while a human or robotic hand stimulus of a particular colour was presented. The task designed such that participants won 90% of trials against a hand of a particular colour and lost 90% of trials against another colour for both the human and robotic hand stimuli. Thus the winning hand was associated with a high reward value and the losing hand was associated with a low reward value. Participants were subsequently required to complete a hand mimicry task. They found that low autistic traits and high empathy predicted greater mimicry of human hands associated with high rewards compared to low rewards. However, no such relationship was present for high-reward vs. low-reward robotic hands. They discuss the hypothesis that individuals with high empathy (and low autistic traits) may find the human hand intrinsically more rewarding, and thus may be more susceptible to the reward value associated with hand stimuli. On the other hand, those with lower empathy (and high autistic traits) may lack an interest in human hands and therefore there was no reward conditioning effect on mimicry. However, they found no correlation between individual traits and mimicry for human or object stimuli once collapsed across the reward conditions. This finding agrees with our lack of correlation for the finger stimulus but disagrees with our finding of low empathy predicting greater imitation of the object. It is therefore possible that the relationship between mimicry and empathy/autistic traits exists only for emotional stimuli such as facial expressions, and is only brought out for non-emotional stimuli such as hands when reward values are assigned to the stimuli. Autistic traits were not measured in the current study; however AQ questionnaires were used in later experiments.

In experiment 1b, participants with higher EQ scores tended to agree with the statement 'seeing the object move made me want to move my own finger' and participants with lower EQ scores tended to disagree with this statement. This is the opposite relationship to that present for experiment 1a for the same question. In addition, participants with higher EQ scores also tended to report that ‘seeing the finger move made me want to move my own finger’, whereas participants with lower empathy scores tended to disagree. One possible interpretation of the lack of agreement between the correlations in experiment 1a and 1b is that participant’s self-report scores may be less reliable in experiment 1b as the RT results suggest participants may have paid less attention to the stimuli due to dual task demands (thus no significant imitative compatibility effects or human bias were present). In line with this, participants with a lower empathy score reported being less aware of whether they were viewing either a hand or an object, whereas those with higher empathy scores reported that they were more aware of the stimulus they were viewing. It is possible that the highly empathetic participants simply scored the questions more highly (for all three questions) due to demand characteristics.

2.1.6 Conclusion

Experiment 1a has replicated previous findings that imitative compatibility effects are stronger for biological relative to non-biological stimuli, supporting the idea that these stimulus types are differentially processed. The results obtained also indicate that as we predicted, imitative compatibility was present using a diffuse go signal at earlier time SOAs. These findings emphasize the important role of attention plays in the emergence of imitative compatibility effects, and the fact that ‘automatic’ imitation is not an automatic process, but is modulated by attention. In addition, experiment 1b indicated that the use of the oddball detection task is not a suitable method to manipulate attention towards the moving stimuli, as the imitative compatibility effects previously observed for the finger stimulus in experiment 1a were removed. One likely explanation is that dual task interference is high due to both tasks being situated in the visual modality. In addition the influence of lateral spatial compatibility appeared to be greater in experiment 1b suggesting the oddball task may have drawn attention to the spatial aspect. We have also found that higher EQ scores were associated with a greater difference between maximum compatibility effects for the finger compared to the object stimulus.

2.2 Experiment 2 - Introduction

In experiment 1b, the visual secondary task of detecting randomly interspersed obvious jumpy movements was designed to direct attention towards the moving stimuli. However conversely the addition of a visual dual task removed the previously observed imitative compatibility effects for the finger stimulus and the human bias of imitative compatibility effects. As discussed in **section 2.1.5.2**, it is possible that the removal of imitation could be due to the fact that both tasks accessed the same sensory modality (visual). Alternatively, although unlikely (since the results suggest participants found the oddball detection task easy), the possibility that the removal of the previously observed effects was due to high cognitive load cannot be ruled out. Therefore, experiment 2 was designed in order to tease apart these two possibilities.

There is some debate among researchers regarding the ‘attentional demands’ of movement observation. Some researchers have argued that the direct-matching mechanism during movement observation is a near-automatic mechanism (Gallese et al., 1996). Some evidence supports this argument. For example, using fMRI Jastorff et al. (2010) aimed to investigate how goal-directed motor acts performed by others are coded within the parietal and premotor cortices of the human brain. Participants were presented with video clips of actors performing four different motor acts (dragging, dropping, grasping and pushing). In addition, participants were asked to perform a secondary attentionally demanding high acuity task (Vanduffel et al., 2002) in order to control for the possibility that more unusual motor tasks captured the participant’s attention more than more commonly performed motor acts, thus eliciting stronger fMRI responses. In the secondary task, the fixation point used was replaced by a horizontal bar which flipped to vertical for 1s at a random interval between 3 - 15s; participants were required to indicate when they saw the flip by pressing a button with their right index finger. They found that movement observation activates neural motor areas to a similar extent whether participants focused on the moving stimuli only (single task); or divided attention between the movement stimulus and a secondary attention-demanding task (dual task).

However, as discussed, behavioural findings suggest that movement observation is influenced by top-down attentional control. For example, studies have suggested that visual attention needs be directed towards the movement of the stimulus to increase the efficiency of movement observation (Bach et al., 2007; Chong et al., 2008). In addition, at a neural level, using whole head MEG recordings, Muthukumaraswamy and Singh, (2008) have shown that brain activity within the movement observation network is enhanced when subjects allocate attention to the movement stimuli, suggesting that cognitive activity enhances movement observation (see **Section 1.6.2** for a more detailed description of this study).

Of particular relevance to the current experiment, is a recent study by Saudeco Marquez et al. (2011), which specifically aimed to investigate the attentional costs related to movement observation (MO), and whether dual-task interference with MO depends on the similarity in the sensory modality of the tasks. Subjects observed movies of an actor lifting objects of different weights (light or heavy), and corticomotor excitability of the muscles involved in the observed actions was measured whilst TMS was applied at the start of the observed movement. Participants performed the weight discrimination task in addition to either a secondary auditory or visual discrimination task (experiment 2). In the auditory task, two tones were presented and participants were asked to verbally indicate whether they were identical or different **(Figure 23a)**. In the visual discrimination task, participants were asked to verbally indicate whether the ‘rhythm’ of colour change of the rim surrounding the movie clips was identical or different **(Figure 23b)**. A baseline condition was included in which no movement was observed and participants were able to fully concentrate on the discrimination task. They found that when a secondary auditory discrimination task was used, corticomotor excitability reflected the force requirements for the observed movies (i.e. no dual task interference took place). However, when a secondary visual discrimination task was used, no modulation of corticomotor excitability was present, suggesting dual task interference took place. These findings clearly indicate that when the secondary task is situated in a separate sensory modality (e.g. auditory), no dual task interference occurs. However, a secondary visual task interfered with the movement observation task.

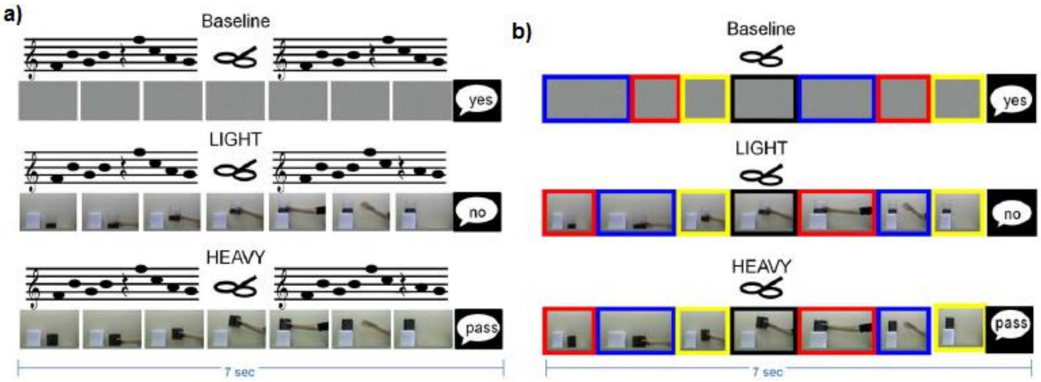

Figure 23: Stimuli used in Saudeco Marquez et al. (2011): **a)** one trial in the auditory discrimination task where a series of two tones was played and participants had to indicate whether they were identical or different; **b)** fone trial in the visual discrimination task in which the ‘rhythm’ of colour change of the rim surrounding the movie clips could either be identical or different.

These results are consistent with our findings in experiment 1b, in which the secondary visual task of monitoring for oddball trials removed the human bias of imitative compatibility effects and the imitative compatibility effect for the finger stimulus. However, a key difference between experiment 1b and the visual task used by Saudeco Marquez (2011) is that in their secondary task, participant’s visual attention was directed towards the changing colour of the rim potentially acting as visual distractors, whereas in experiment 1b the location of the movement observation task and the secondary oddball task were the same, potentially drawing more attention towards the movement. The results of experiment 1b complement their finding that performing a secondary visual task simultaneously reduces performance in the movement observation task, and further suggest that this is the case even when visual attention is directed towards the location of the observed movement. This reinforces their conclusion that the absence of weight related modulation of M1 excitability when using a secondary visual discrimination task was likely to be due to the fact both tasks were drawing on common resources, as opposed to participants simply being visually distracted away from the location of the observed movement. In addition, their results strongly indicate that when a secondary task involves a different sensory modality (auditory), no dual task interference was present.

Therefore, in experiment 2, we investigated whether imitative compatibility effects would be present in an experiment using a secondary auditory task. The results of experiment 2 can be compared to experiment 1b in which performing a secondary visual task whilst performing the imitative compatibility task, removed the imitative compatibility effects. Based on Saudeco Marquez et al. (2011) results, we hypothesized that imitative compatibility effects would be present whilst performing a secondary auditory task, which would suggest that the dual task interference in experiment 1a was due to both tasks being in the same sensory modality.

In this experiment we also included the autism spectrum quotient (AQ) questionnaire in addition to the (EQ) empathy questionnaire, as discussed in **Section 2.1.5.3**. We hypothesized that consistent with experiment 1a, that there may be a negative relationship between EQ scores and maximum compatibility effects for the object. In addition, although not present in experiment 1a, one might expect to see a positive relationship between EQ scores and maximum compatibility effects for the finger if more empathetic participants are more drawn to biological motion. Since EQ and AQ scores have been found to be strongly negatively correlated, conversely one might expect a positive correlation between AQ and compatibility effects for the object, and a negative correlation between AQ and compatibility effects for the finger.

2.2.1 Methods

2.2.1.1 Participants

20 right-handed healthy individuals (12 female), with a mean (±SD) age of 22.15 (±3.22) years were recruited. The mean (±SD) laterality quotient was 88.20 (±17.84). The study consisted of a single testing session lasting approximately 1 hour, and participants were paid £5 for their participation.

2.2.1.2 Design and procedure

The apparatus, stimuli, and design and procedure were all identical to that described in experiment 1b. However, the randomly interspersed jumpy oddball trials used in experiment 1b were replaced with trials in which an auditory ‘beep’ tone was played for 40ms. The auditory tone was generated on Audacity software (Waveform: sine; Frequency (Hz): 800; Amplitude: 1; Duration 40ms). During ‘beep’ tone trials, no yellow flash was presented. Participants were required to say the word ‘beep’ when then they heard the beep tone. As in experiment 1, participants were required to complete the ELI questionnaire for handedness **(Appendix A1)** and the EQ empathy questionnaire **(Appendix A2)** and an additional self-reported questionnaire regarding perception of stimulus differences, as detailed in **section 2.1.2.4**. Participants were also required to complete the AQ questionnaire (Baron-Cohen et al., 2001) **(Appendix A3)**.

2.2.2 Results

2.2.2.1 Analysis of error data

The same exclusion criterion detailed in **section 2.1.3.1** was used for the removal of RTs. This resulted in a total loss of 2.23% of trials on average. In addition, the same error types were present as those described in **section 2.1.3.1**.

Overall, participants in both groups made a low level of errors **(section 2.1.3.1; Table 3 and Table 7)**; therefore no individual participant's data was removed from the study. The error which participants were most prone to was the oddball + button press error. All participants correctly identified 100% of the beep tone trials and no false alarms were made.

Table 7: Mean % no-go and anticipation errors (±SE) for each condition. No-go errors were made out of a potential 80 and anticipation errors were made out of a potential 640. **Bold** type represents compatible trials.

Stimulus	**View**	**Mean No-go errors (±SE)**	**Mean Anticipation errors (±SE)**
Finger	Mirror	**0.18 (± 0.07)** 0.15 (± 0.06)	**2.03 (± 0.04)** 2.19 (± 0.04)
	Anatomical	**0.35 (± 0.10)** 0.20 (± 0.06)	**1.25 (± 0.02)** 1.25 (± 0.02)
Object	Mirror	**0.08 (± 0.35)** 0.18 (± 0.55)	**0.31 (± 0.01)** 1.41 (± 0.03)
	Anatomical	**0.28 (± 0.68)** 0.15 (± 0.43)	**2.34 (± 0.05)** 2.18 (± 0.04)

2.2.2.2 Analysis of reaction time data

Overall mean RTs (ms) (± SE) are presented in **Table 8.** Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects.

Table 8: Mean RTs (ms) ± (SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (p<.05).

Stimulus	View	Response	SOA (ms)	Mean RT (ms) (± SE)
Finger	Mirror	Press	0	**347.31 (± 16.71)** 377.75 (± 24.75)*
			120	**317.65 (± 13.31)** 324.45 (± 18.00)
			280	**307.10 (± 15.17)** 311.19 (± 18.78)
		Release	0	**358.90 (± 17.26)** 357.40 (± 19.56)
			120	**317.31 (± 13.65)** 330.80 (± 12.91)
			280	**300.68 (± 9.93)** 302.90 (± 8.91)
	Anatomical	Press	0	**362.61 (± 15.18)** 359.37 (± 18.65)
			120	**326.61 (± 15.43)** 329.24 (± 18.03)
			280	**297.43 (± 13.59)** 314.73 (± 14.40)
		Release	0	**346.60 (± 15.00)** 357.65 (± 16.33)*(p=.079)*
			120	**308.96 (± 12.80)** 326.33 (± 14.37)*
			280	**304.92 (± 11.48)** 299.56 (± 14.07)
Object	Mirror	Press	0	**378.87 (± 20.88)** 352.91 (± 16.81)*
			120	**334.50 (± 17.74)** 341.87 (± 18.93)
			280	**305.90 (± 12.98**) 310.93 (± 16.15)
		Release	0	**361.24 (± 17.08)** 370.71 (± 18.58)
			120	**325.35 (± 11.38)** 332.12 (± 12.17)
			280	**296.82 (± 11.01)** 311.86 (± 12.17)*
	Anatomical	Press	0	**368.86 (± 17.57)** 350.21 (± 16.83)* *(p = .073)*
			120	**330.34 (± 15.11)** 326.85 (± 13.71)
			280	**315.42 (± 15.46)** 301.91 (± 13.84)* (*p*= .053)
		Release	0	**371.58 (± 20.26**) 366.74 (± 17.88)
			120	**321.09 (± 14.92)** 324.85 (± 13.62)
			280	**294.74 (± 10.04)** 302.19 (± 10.75)

An initial ANOVA was conducted on participants mean RTs; with view (mirror/anatomical) x stimulus (hand/object) x compatibility (compatible/incompatible) x SOA (0, 120, 280) x response (press/release). There were a number of significant interactions with response types; therefore, pressing and releasing responses were analysed separately.

An ANOVA for pressing responses was conducted. There was the usual main effect of SOA (*F*(2,38) = 60.181, *p* = .000). There was a two-way interaction between stimulus and compatibility (*F*(1,19) = 6.531, *p* = .019), a three-way interaction between stimulus, compatibility and SOA (*F*(2,38) = 3.744, *p* = .033), and a four-way interaction between view, stimulus, SOA and compatibility (*F*(2,38) = 4.469, *p* = .018). In order to analyse this four-way interaction, two separate sub-ANOVAs were conducted on mean RTs for the mirror view and the anatomical view; with stimulus, SOA and compatibility as within-subjects factors. There was a significant interaction between stimulus, SOA and compatibility for the mirror view (F(2,38) = 7.305, *p* = .002). No such interaction was present for the anatomical view (*F*(2,38) = 1.015, *p* = .362). A follow up t-test on compatibility effects for the finger compared to the object stimulus at each SOA in the mirror view, revealed there was a significant difference between compatibility effects for the finger (M = 30.44ms) and the object (M = -25.96ms) at 0ms **(Figure 24)**; however, there was no significant difference between compatibility effects for the finger and object at the 120ms and 280ms SOAs .

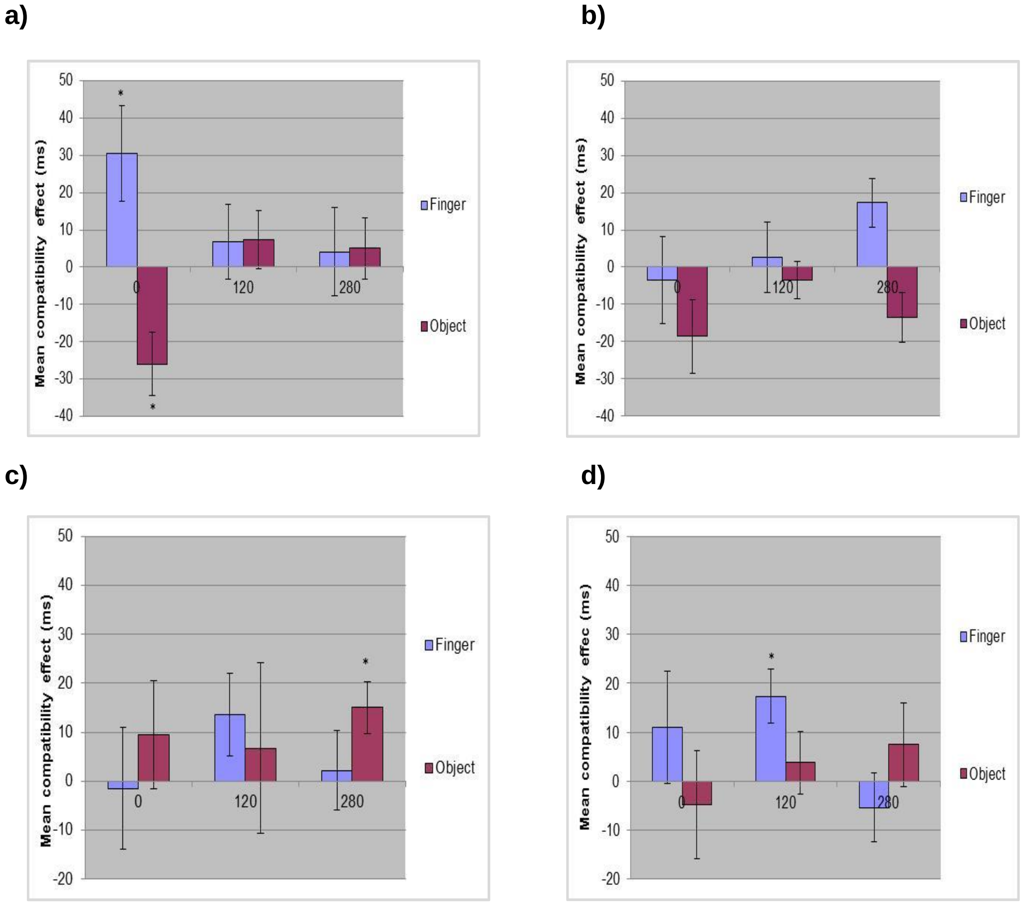

Figure 24: Compatibility effects for the finger and object: **a)** mirror view (pressing responses); **b)** anatomical view (pressing responses); **c)** mirror view (releasing responses); **d)** anatomical view (releasing responses).

For pressing responses, paired t-tests between compatible and incompatible RTs in each individual condition showed significant compatibility effects were present for: 1) 0ms in the mirror view for the finger stimulus; 2) 0ms in the mirror view for the object stimulus (reverse compatibility effect). In addition, the following compatibility effects were approaching statistical significance: 1) the reverse compatibility effect for the object at 0ms in the anatomical view and 2) the compatibility effect for the object at 280ms in the anatomical view **(Table 8)**.

An ANOVA for releasing responses was also conducted, revealing the usual main effect of SOA (*F*(2,38) = 44.063, *p* =. 000) and a main effect of stimulus (*F*(1,19) = 5.874, *p* = .026), indicating that RTs for the finger (M = 329.81ms) were significantly faster than RTs for the object (M = 335.50ms). There was also a main effect of compatibility (*F*(1,19) = 23.139, *p* = .000) indicating compatible reactions (M = 329.39ms) were significantly faster than incompatible RTs (M = 335.91ms).

For releasing responses, paired t-tests between compatible and incompatible RTs in each individual condition showed significant compatibility effects were present: 1) for the finger stimulus at 120ms in the anatomical view, and; 2) for the object stimulus at 280ms in the mirror view. The compatibility effect for the finger stimulus at 0ms in the anatomical view was approaching statistical significance **(Table 8)**.

Paired t-tests comparing compatible and incompatible RTs at 0ms with baseline RTs were carried out in order to determine whether the observed compatibility effects resulted from the facilitation of compatible movements, interference from incompatible movements, or a combination of facilitation and interference. At 0ms SOA there was a significant compatibility effect for the finger in the mirror view (pressing response), but not in the anatomical view; therefore only the mirror view 0ms RTs were compared with mirror view baseline RTs for the pressing response.

A paired t-test between compatible and incompatible RTs for the finger (mirror view, pressing response) at 0ms and baseline (mirror view, pressing response) RTs showed that the difference between compatible RTs (M = 347.31ms) and baseline RTs (M = 370.42ms) was approaching significance (*t*(19) = -2.088, *p* = .051); however there was no significant difference between incompatible RTs and baseline RTs (*t*(19) = .474, *p* = .641). This indicates that facilitation of compatible RTs is likely to be responsible for the compatibility effect observed at 0ms **(Figure 25).**

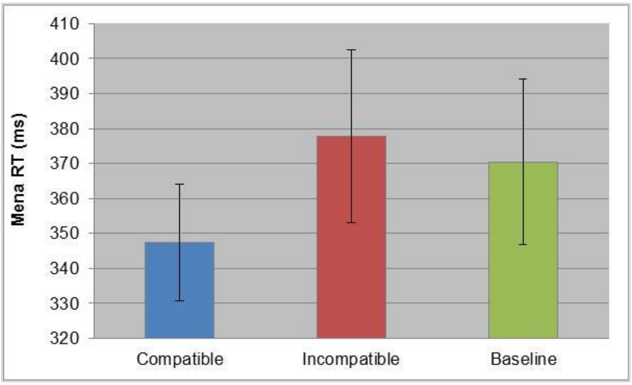

Figure 25: Difference between baseline RTs and compatible/incompatible RTs at 0ms SOA (mirror view) for the finger stimulus. The difference between incompatible and baseline RTs was approaching significance.

2.2.2.3 Comparison of compatibility effects in experiment 1 and experiment 2

Figure 26 was included to provide a visual comparison between compatibility effects in experiment 1a compared to experiment 2. To investigate whether compatibility effects differed significantly between experiments 1a and 2, a repeated measures ANOVA was conducted on participant’s mean compatibility effects with response x view x stimulus x SOA as within subjects factors and experimental group (experiment 1a or 2) as a between-subjects factor.

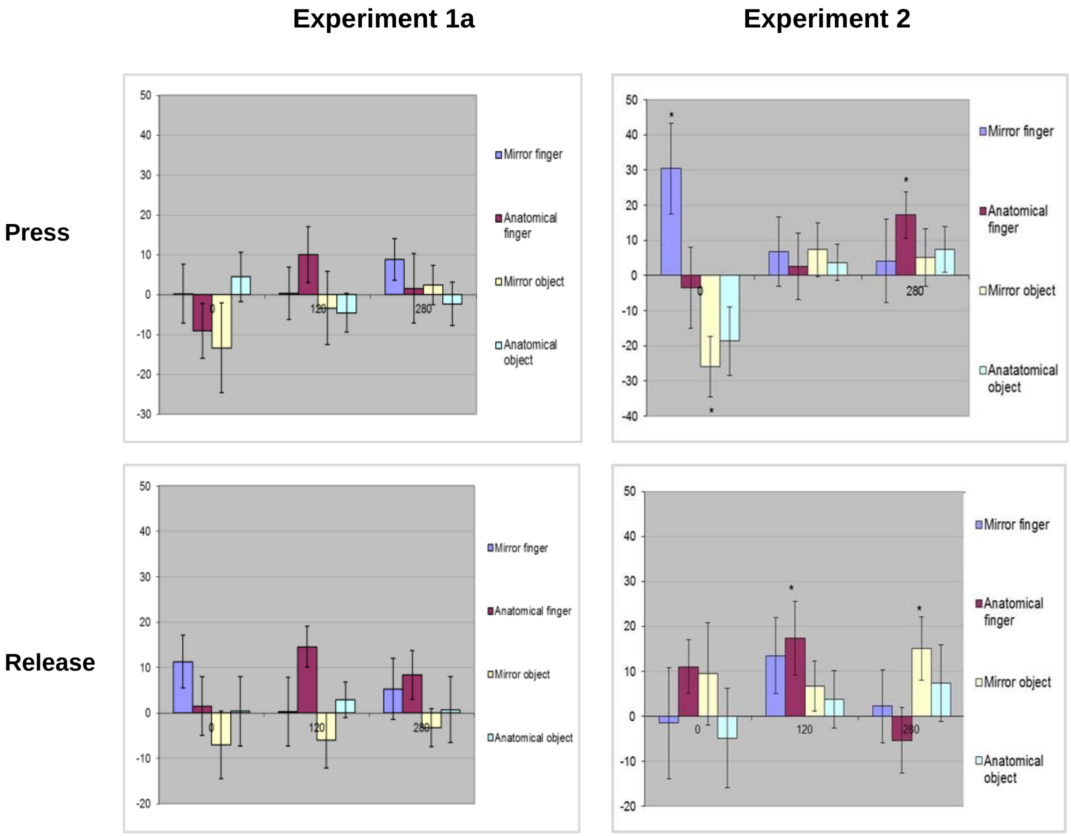

Figure 26: Charts show imitative compatibility effects for each stimulus and view across the SOAs for pressing and releasing responses in experiment 1a compared to experiment 2.

The initial ANOVA revealed there was a significant three-way interaction between response, stimulus and experimental group (*F*(1,38) = 4.419, *p* = .042). The four-way interaction between response, stimulus, SOA, compatibility and experimental group was approaching significance (*F*(2, 76) = 2.775, *p* = .069). In order to analyse the significant three-way interaction two separate sub-ANOVAs were conducted for pressing and releasing responses. For releasing responses no interactions involving compatibility and experimental group were present. For pressing responses there was a significant interaction between stimulus, SOA and experimental group (*F*(2,76) = 3.510, *p* = .035). Paired t-tests on compatibility effects for each stimulus and SOA between the two experimental groups revealed that compatibility effects were significantly stronger in experiment 2 (M = 13.48ms) compared to experiment 1a (M = -4.42) for the finger stimulus at an SOA of 0ms (*t*(19) = -2.476, *p* = .023).

A repeated measures ANOVA to investigate whether compatibility effects differed significantly between experiments 1a and 1b was also conducted on participant’s mean compatibility effects with response x view x stimulus x SOA as within subjects factors and experimental group (experiment 1a or 1b) as a between-subjects factor; however no interactions between experimental groups were found, indicating that there were no significant differences between compatibility effects in experiment 1a and 1b.

2.2.2.4 Analysis of questionnaire data

Mean self-reported questionnaire scores are reported in **Table 6.** As no formal hypotheses were developed for self-reported questionnaire data findings in this experiment, the discussion of these findings have been included in **Appendix B1**.

2.2.2.4.1 Exploring the relationship between EQ/AQ scores and maximum imitative compatibility effects

A Pearson's correlation test was conducted between each participant's EQ questionnaire score and each participant's maximum compatibility effect for the finger and object; however no significant correlations were found (*r*(20) < -.061, *p* > .799).

A Pearson's correlation test between participants AQ scores and each participant's maximum compatibility effect for the finger and object revealed that the positive correlation between maximum compatibility effects the object and AQ scores was approaching significance (*r*(20) = .428, *p* = .060) **(Figure 27)**.

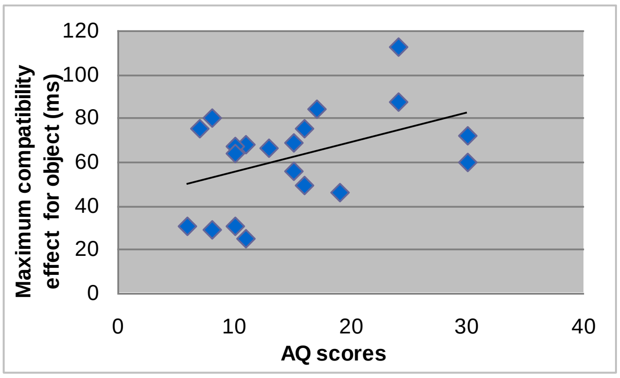

Figure 27: Positive correlation between maximum compatibility effects for the object and AQ scores was approaching significance

2.2.3 Discussion

Experiment 2 has revealed a number of interesting findings. In line with our predictions, imitative compatibility effects for the finger were present when an auditory secondary task was used. As imitative compatibility for the finger was absent in experiment 1b, where a visual secondary task was used, this supports the hypothesis that imitative compatibility effects may be removed when the secondary task used is visual, due to the fact both tasks are situated the same sensory modality. In experiment 1b the secondary visual task interfered with movement observation and action perception coding; and was prioritised over the imitation task leading to the removal of imitative compatibility effects. However, less dual task interference was present in experiment 2 using an auditory secondary task, thus significant imitative compatibility effects for the finger were produced. This suggests a secondary task in a different sensory modality does not interfere with movement observation and action-perception coding. Moreover, the comparison between imitative compatibility effects for experiment 1a and experiment 2 indicates that imitative compatibility effects were stronger in experiment 2 compared to experiment 1a for the finger, suggesting a possible facilitation of imitative compatibility relative to a baseline level of inhibition of imitative compatibility effects in the control version task. Interestingly, a significant imitative compatibility effect was also present for the object stimulus (mirror, releasing response, 280ms); although a reverse effect was also present for the object (mirror, pressing response, 0ms) in the auditory dual task condition. In addition, we have not found any significant correlations between EQ scores and each participant's maximum compatibility effect; however the correlation between maximum imitative compatibility effects for object and AQ scores was approaching significance. These findings will now be discussed in further detail.

2.2.3.1 Importance of the sensory modality of the secondary task

In experiment 2, we have observed that the use of a secondary auditory task produces imitative compatibility effects, suggesting that little or no dual task interference took place when the secondary task accessed a separate sensory modality to the imitation task. This replicates Saudeco Marquez et al. (2011) TMS findings that when the secondary task involved a different sensory modality (auditory) the observers' motor system may respond in a near automatic manner, whereas interference with MO arises when competing visual stimuli are present. As hypothesized this finding suggests that the loss of imitation in experiment 1b, which used a secondary visual oddball detection task, was due to the fact that the secondary task accessed the same sensory modality (visual) as the automatic imitation task, and confirms that the previous loss of imitation was not due to the general 'cognitive load' of utilising a dual task procedure. Together, these findings strongly suggests that dual task interference with action observation arises when 'competing' visual stimuli are present. However, when the secondary task is situated in a separate sensory modality (auditory) no dual task interference with MO takes place.

It is interesting that in Muthukumaraswamy and Singh (2008) study (described in **section 1.7.2**), the maths task (which also involved visually paying attention to the movement) did not have this effect. Conversely, they found that activity in the MNS is enhanced by attention to the masks task. In their discussion of these results they discussed alternative interpretations for the enhanced desynchronization in the maths task. For example, they discussed the possibility that in the maths condition participants might have been using a covert motor strategy to perform the task causing the increased activity in the sensorimotor cortex. Although they indicate none of the participants reported that they had not felt that they used a motor strategy to perform the task, they admitted that it is possible that this may have occurred outside of participant's conscious awareness. In addition, a key difference is that in experiment 1b, participants were required to detect the yellow flash and respond by pressing or releasing the button, in addition to detecting the oddball movements. In contrast, in their experiment, participant's attention was fully focused on the observation of the movement in order to complete the imitation/maths task with no concurrent detection or motor task. Therefore, it is possible that the activity of the MNS is inhibited when participants are required to focus on the movement while additionally carrying out a motor task.

Another possibility is that participants were paying such close attention to detecting oddball movements they were consequently paying less attention to the overall direction of the movement, thus removing imitative compatibility effects. In the maths task, attention was drawn to the stimuli but not particularly to detailed aspects of the movement of the stimuli. This is a similar concept to the idea that if participant's attention is drawn to the fact that movements are going to differ (e.g. in studies where participants are instructed that an observed action will either be biomechanically possible or biomechanically impossible) attention may shift to the kinematic aspect of the movement. Since in movement compatibility paradigms the direction of movement is responsible for the imitative compatibility effect, drawing attention towards kinematics might reduce the overall imitative compatibility effects produced.

2.2.3.2 Possible enhancement of imitative compatibility effects due to auditory task

Interestingly, the results of experiment 2 suggest that having a dual auditory task interfered less with imitative compatibility effects than a dual visual task. On visual comparison imitative compatibility effects may have actually been stronger in experiment 2 compared to experiment 1a for both stimuli. We have found that the imitative compatibility effects at 0ms for the finger stimulus were significantly stronger in experiment 1a compared to experiment 2. This provides evidence that performing a secondary task situated in a different modality might facilitate imitative compatibility effects. Although it must be noted that these experiments involve separate groups of participants, a comparison of mean RTs shows that there is a significant difference in RTs between all three experiments. As would be expected, the fastest RTs were in experiment 1a (M = 323.52ms) when no secondary task was used. Mean RTs were slower during the dual auditory task condition (M = 331.03s) however the difference between RTs in experiment 1a and 2 was not significant (*t*(19) = -.352, *p* = .729). Mean RTs were slowest in the dual visual task condition (M= = 381.72); this was significantly slower than mean RTs in experiment 1a (*t*(19)= -2.536, *p* =.020) and experiment 2 (*t*(19) = 3.313, *p* =.004). The fact that mean RTs were faster in the auditory task condition compared to the visual task condition supports the idea the participants found the task auditory task easier due to the fact it was in a different sensory modality. Participant's ability to detect the beep tone was 100% as opposed to 98% on average for detection of oddball trials in experiment 1b, which also indicates the auditory task may have been easier than the oddball detection task. In addition, there was a significant difference between baseline RTs for experiment 1b (M = 423.57ms) and both experiment 1a (M = 356.25ms) (*t*(19) = -2.561, *p* = .019) and experiment 2 (M = 363.22ms) (*t*(19)=2.020, *p* = .007). However, there was no significant difference between experiment 1a (M = 356.25ms) and experiment 2 (M = 363.22ms) (*t*(19) =-.284, *p* = .780). If it is assumed that the participant groups were similar across these three experiments, the fact RTs were slower in experiment 1b even in the baseline condition indicates that overall cognitive load may have been higher in the oddball task relative to the auditory task, leading to overall slower baseline RTs. However, considering that RTs were different in experiment 1b at baseline compared to the other experiments, we cannot exclude the possibility that the participants also had overall generally slower RTs compared to participants in experiments 1a and 2. The fact that baselines RTs are similar in experiments 1a and 2 indicates that the differences observed between the experiments are not likely to be due to different groups of participants.

One possible interpretation of a potential facilitation effect due to the secondary auditory task is that responding out loud could have enhanced self-focus compared to when completing the imitative compatibility task silently. This is because having the secondary task of identifying the auditory beep trials might have made the participant more aware of the experimenter’s presence, and an audience of even a single observer has been shown to enhance self-focus (Carver and Scheier, 1978). Additionally, hearing voice recordings of one’s own voice has been shown to enhance self-focus (however it should be noted there is no clear evidence to my knowledge that this finding can be extrapolated to hearing one’s own voice as they speak out loud). A recent study has shown that self-focus enhances imitative compatibility effects (Spengler et al., 2010b) therefore raising the possibility that increased self-focus due to the auditory task may have led to enhanced imitative compatibility effects. Interestingly, a study has found that responses to imitative actions are much less slowed compared to responses to spatial cues, when simultaneously articulating a word compared to when not verbalising (Kühn and Brass, 2008). Based on fMRI studies which have shown an overlap in brain areas involved in speech and finger imitation (Broca’s area), they suggested that pre-activation of Broca’s area due to speech may facilitate imitation due to shared functional mechanisms.

However, the current results suggest an alternative simpler explanation for this finding, whereby the addition of a secondary task may occupy resources previously used for inhibiting imitation, thereby causing disinhibition of the ‘baseline’ level of inhibition. The fact that imitative compatibility effects for the finger produced in this experiment were stronger than those observed in experiment 1a, supports the possibility that in the control situation (experiment 1a) there is a baseline level of inhibition present for both stimuli. In experiment 2, it is possible that the auditory task occupied cognitive resources that were previously allocated to the inhibition of imitation and differentiating between stimulus types, consequently reducing the level of baseline inhibition and thus facilitating imitation. The comparison of RTs at 0ms and baseline support the current interpretation as the results indicate that the compatibility effects present were due reduced inhibition of imitation (faster RTs from viewing imitatively compatible trials). This idea would be consistent with theories that propose MNS modulation may occur as a method of controlling inappropriate or unwanted imitation (Spengler et al., 2009). However, the current results suggest that a secondary auditory task may interfere with the ability to control imitation.

As an alternative to looking at patients with frontal lobe damage (which as previously discussed **(section 1.7)** is known to cause increased spontaneous imitative behaviours), van

Leeuwen et al. (2009a) have suggested that increasing working memory load in healthy populations may provide an alternative method of producing same effect. This hypothesis is based on research that suggests in studies of frontal lesion patients with fronto-lateral damage were more prone to increased spontaneous imitation (Lhermitte et al., 1986), an area which has been suggested to be important in executive processing, including processes dependant on working memory (e.g. information retention, response selection and information verification) (Owen et al., 2005). To explore this hypothesis further, van Leeuwen et al. (2009a) used an adapted version of Brass et al. (2000) automatic imitation paradigm, and included an executive function secondary task with either a high or low working memory manipulation. They hypothesized that by occupying working memory, executive capacities normally available to control imitative compatibility behaviour would be reduced, possibly leading to facilitated imitative compatibility. In this experiment participants watched clips of a human hand performing finger movements, and were required to make movements with their own fingers. In their 'baseline' condition participants had to either imitate the finger movement (finger cue) or move the finger on which an 'X' appeared (spatial cue). In their non-baseline condition, both a finger movement occurred and an X appeared, and depending on the prior instruction given participants had to respond to one of the cues and ignore the other. They hypothesized that increasing working memory load would reduce the usual inhibitory suppression of spontaneous imitation of the finger movement. However they predicted increased load should not interfere with executing spatially cued finger movements because it is not an automatic response. Their results indicated that increased working memory load facilitated RTs to finger cues, while responses to the spatial cues remained unchanged. Their results are of particular relevance to the current findings, as they suggest that increased attention to another task reduces the baseline level of inhibition of imitation (possibly by occupying resources to inhibit latent imitative responses and therefore facilitating imitative compatibility).

Taken together, the findings in experiments 1 and 2 can support the following explanation: 1) a baseline level of inhibition and active differentiation between stimulus types may occur when no dual task is added (experiment 1a), 2) imitative compatibility effects may be facilitated by a dual auditory task which may occupy attentional resources, thus reducing the resources available for inhibition of imitation in experiment 2, and 3) a visual dual task may interfere with perception-action coding due to the fact both tasks are visual, thus the visual dual task competes for shared resources, removing imitative compatibility effects (experiment 1b).

2.2.3.3 Relationship between maximum compatibility effect for the object and AQ scores

Although we did not find any significant correlations between EQ scores and each participant's maximum compatibility effect in this experiment, a positive correlation between maximum imitative compatibility effects for object and AQ scores was approaching significance. We hypothesized that high autistic traits may predict lower compatibility effects for biological motion. The near significant correlation fits in with this hypothesis as it suggests high autistic traits predict greater imitation of non-biological stimuli, but not biological stimuli, suggesting a possible preference for non-biological relative to biological motion.

2.2.4 Conclusion

Experiment 2 has revealed that imitative compatibility effects are present, and appear to be enhanced when a secondary auditory task was performed simultaneously. This suggests that the removal of imitative compatibility effects in experiment 1b was due to both tasks involving the visual modality, as opposed to general cognitive load. It suggests that dual visual task may interfere with imitative compatibility processing. The enhancement of imitative compatibility when an auditory dual task is used supports the idea that when no dual task is added there may be a baseline level of inhibition of imitation.

2.3 Experiment 3 - Introduction

As previously discussed in **section 1.5,** there is some debate as to what extent the processing of biological motion is 'special' relative to non-biological motion. It has been suggested that the 'human bias' that is often attributed to preferential processing of biological stimuli by the MNS could be explained by physical differences between biological and non-biological stimuli, such as stimulus saliency (Jansson et al., 2007). Gowen and Poliakoff (2012) top-down attentional model, described in **section 1.8**, suggests that differentiation between biological and non-biological stimuli may be an active process. According to this model imitation of human stimuli may be 'special' in the sense our brains may be tuned to integrate and compare stimulus properties (such as appearance, kinematics or prior knowledge/context) and modulate the extent of imitation based on the degree of similarity with oneself. This model also suggests that imitation of non-biological stimuli may be dependent on attention, such that if attention is drawn to the non-biological characteristics of the stimulus, imitation of the non-biological stimulus may be inhibited.

It has been observed that when biological and non-biological stimuli are presented randomly mixed within a block of trials, imitative compatibility for non-biological stimuli are less likely to be significant (Gowen and Poliakoff, 2012). In contrast, significant imitative compatibility effects for non-biological stimuli have been observed in a number of studies in which stimuli are presented in separate blocks of trials. Gowen and Poliakoff (2012) suggested that this emerging trend could be explained by differences in attention. When biological and non-biological stimuli are presented mixed within blocks of trials (as in experiment 1a) this may draw attention to the differences/contrast between the biological and non-biological stimuli, leading to an inhibition of imitative compatibility for the non-biological stimulus, and enhanced imitation of the biological stimulus. Conversely, when stimuli are presented in separate blocks, less attention is drawn to stimulus differences, allowing imitative compatibility to emerge for the non-biological stimulus.

However, an alternative explanation for this finding is that if participants see the human stimulus prior to seeing the non-biological stimulus, it is possible that a carry-over effect of agency may occur due to participants associating the non-biological stimulus with the previously observed movement, causing imitative compatibility effects to be present for the object stimulus. In support of this idea a number of studies have found that beliefs regarding stimulus agency and prior knowledge affect imitative compatibility effects (see **section 1.7.3** for a review of the previous literature on the effect of prior knowledge/beliefs regarding stimulus agency on imitative compatibility effects).

Experiment 1a replicated previous findings of a stronger imitative compatibility effect for biological stimuli compared to non-biological when both biological and non-biological stimuli were presented mixed within blocks of trials. In experiment 1b we attempted to increase participant's attention toward stimulus movement by asking participants to identify oddball movements, however, the addition of this secondary task removed all imitative compatibility effects. Therefore, in experiment 3, we used a more subtle method of manipulating attention between stimulus types, by presenting the hand and object stimuli in separate 'pure' blocks of each stimulus type. We also examined whether the order in which the stimuli are presented (finger first or object first) had an effect on imitative compatibility effects. If imitative compatibility for the object is present in the finger first group, but not in the object first group, this would suggest seeing the finger prior to seeing the object may cause participants to associate the object movement with a finger movement (causing imitation of the object stimulus to be present). Our first aim was to determine whether there would be a difference in imitation when stimuli were presented in separate blocks compared to experiment 1a, where stimuli were randomly mixed within a block of trials using the current paradigm. Based on previous studies we expected to see a reduced human bias and imitative compatibility effects to be present for the object. Secondly, we aimed to determine which of the two possible hypotheses was likely to be the cause of any such differences in imitative compatibility between the mixed and blocked conditions. We hypothesized that if differences were caused by associating the non-biological stimulus with the human stimulus we would only expect to see imitation of the object in the group of participants who saw the hand first. In contrast, if the differences were caused by decreased attention to stimulus differences in the blocked group, we would the effect to be present across all participants (i.e. we would not expect to see differences between the group of participants who saw the object first and the group of participants who saw the hand first).

2.3.1 Methods

2.3.1.1 Participants

24 right-handed healthy individuals (22 female), with a mean (±SD) age of 19.42 (±0.97) years were recruited. The mean (±SD) laterality quotient was 88.61 (±14.47). The study consisted of a single testing session lasting approximately 1 hour, and participants were paid £5 for their participation.[1]

2.3.1.2 Design and procedure

The experimental set up was identical to that of experiment 1a (control group), however here the stimuli were not presented randomly intermixed within blocks, but as pure blocks of only one stimulus type, followed by pure blocks of the second stimulus type. As in experiment 1a, participants were informed that they would be observing video clips of a moving finger or clips of a moving object, depending on which stimulus the participant viewed first. The participant was not informed that they would be observing the second stimulus type until halfway through the experiment, prior to viewing the second stimulus. The number of trials used was also identical to the number of trials used in experiment 1a. The 720 trials were split into 20 blocks of 36 trials (10 blocks of 36 finger only trials + 10 blocks of 32 object only trials = 720 trials). Oddball trials were included as no-go trials for consistency with experiment 1a. In Blocks 1-10 only the finger stimulus or only the object stimulus was presented. In blocks 10-20 the stimulus they had not already observed in the first half of the experiment was presented. For half of the participants (n=12) the finger stimulus only was presented first, and for the other half (n=12) the object stimulus was presented first. In each group (finger first/object first) half (6) started with releasing for blocks 1-5 and 10-15 then switched to pressing for blocks 6-10 and 15-20; the other half (6) started with pressing and switched to releasing for these blocks.

All participants completed 8 practice trials (6 go/2 no-go) at the start of the experiment, and each time the response type was switched (4 times in total), giving a total of 32 practise trials throughout the course of the experiment. This allowed the participants to become familiar or refamiliarise themselves with the task and required response. A short 'rest' period was given every 36 trials, indicated by a message on the laptop monitor. Participants were able to choose the length of this rest period (typically a minute or two) before continuing onto the next block. Consistent with experiment 1a participants were required to complete the ELI questionnaire for handedness, EQ2 empathy questionnaire and an additional self-reported questionnaire regarding perception of stimulus differences, as detailed in **section 2.1.2.4**.

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[1] It should be noted that the data in experiment 3 was collected by a third year undergraduate student, who was trained in conducting the experiment and supervised by myself and Ellen Poliakoff.

2.3.2 Results

2.3.2.1 Analysis of error data

The same exclusion criterion as described in **section 2.1.3.1** was used for removal of RTs. This resulted in a total average loss of 2.09% of trials. In addition the same error types were present as those described in **section 2.1.3.1**.

Overall, participants made a low level of errors **(Table 3 and Table 9)**; therefore no individual participant's data was removed from the study. The error participants were most prone to was the no-go error. These occurred in all conditions but were more frequent for the finger stimulus in compatible trials viewed from mirror orientation.

Table 9: Mean % no-go and anticipation errors (± SE) for each stimulus. No-go errors were made out of a potential 80 and anticipation errors were made out of a potential (640). **Bold** type represents compatible trials.

Stimulus	**View**	**Mean No-go errors (± SE)**	**Mean Anticipation errors (+ SE)**
Finger	Mirror	**0.58 (± 0.16)** 0.33 (± 0.10)	**2.34 (± 0.03)** 2.19 (± 0.04)
	Anatomical	**0.21 (± 0.10)** 0.29 (± 0.09)	**3.44 (± 0.04)** 3.43 (± 0.03)
Object	Mirror	**0.42 (± 0.16**) 0.46 (± 0.19)	**2.19 (± 0.03)** 2.03 (± 0.04)
	Anatomical	**0.42 (± 0.16)** 0.17 (± 0.08)	**3.28 (± 0.03)** 3.13 (± 0.03)

2.3.2.2 Analysis of reaction time data

Overall mean RTs (ms) (± SE) are presented in **Table 10.** Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects.

Table 10: Mean RTs (ms) (± SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (*p*<.05).

Stimulus	View	Response	SOA (ms)	Mean RTs (ms) (± SE)
Finger	Mirror	Press	0	**440.60 (± 18.02)** 450.08 (± 18.16)
			120	**406.29 (± 14.77)** 404.64 (± 14.46)
			280	**376.65 (± 13.66)** 386.02 (± 16.40)
		Release	0	**317.67 (± 10.82)** 317.63 (± 10.45)
			120	**286.73 (± 7.98)** 294.23 (± 7.22)
			280	**270.67 (± 7.05)** 267.57 (± 8.16)
	Anatomical	Press	0	**445.64 (± 18.05)** 442.31 (± 18.16)
			120	**411.58 (± 16.69)** 411.44 (± 14.18)
			280	**370.13 (± 13.53)** 388.37 (± 14.96)
		Release	0	**323.73 (± 9.48)** 328.14 (± 12.00)
			120	**286.76 (± 8.61)** 299.11 (± 8.91)
			280	**273.00 (± 9.23)** 260.48 (± 7.12)
Object	Mirror	Press	0	**422.26 (± 15.70)** 421.78 (± 13.07)
			120	**394.51 (± 10.82)** 393.27 (± 11.87)
			280	**362.07 (± 13.00)** 365.96 (± 11.54)
		Release	0	**309.74 (± 8.01)** 320.82 (± 9.99)
			120	**279.93 (± 9.23)** 291.01 (± 7.12)
			280	**250.30 (± 7.82)** 269.26 (± 7.84)
	Anatomical	Press	0	**415.46 (± 11.98)** 423.14 (± 13.73)
			120	**398.11 (± 13.67)** 386.39 (± 11.36)
			280	**367.51 (± 13.09)** 364.65 (± 11.64)
		Release	0	**316.29 (± 9.56)** 318.81 (± 11.11)
			120	**286.94 (± 9.41)** 293.19 (± 9.41)
			280	**261.77 (± 8.20)** 262.10 (± 8.93)

An initial mixed design repeated measures ANOVA; with response type (press/release), stimulus (hand/object), compatibility (compatible/incompatible), SOA (0, 120, 280) as within-subjects factors, and group (finger first/object first) as a between subjects factor was conducted on participants' mean RTs. The ANOVA revealed that there was a significant main effect of response type (*F*(1,23) = 224.78, *p* = .000), with release responses being significantly faster (M = 291.08ms) than press responses (M = 403.04ms). There were also significant and significant interactions with response type, including a borderline significant four-way interaction between response, stimulus, SOA and compatibility. Due to the significant main effect and interactions with this factor, mean RTs were analysed separately for press and release responses.

It should be noted that in the initial ANOVA no significant interactions between group and compatibility were present; however, Experiment 3 (which was conducted by a third year undergraduate student) was analysed following the results of experiment 4 in which an effect of group (finger first/object first) was present. Based on the prior hypothesis that significant imitative compatibility effects for the object stimulus would be present in the finger first group only (as in Experiment 4), data for the finger first/object first groups were analysed separately in the experiment 3 in order to further investigate this hypothesis. Therefore, four repeated measures ANOVAs were carried out; 2 ANOVAs for pressing responses with a separate ANOVA for each group (finger first group/object first group), and 2 ANOVAs for releasing responses (with a separate ANOVA for each group); with view, stimulus, compatibility and SOA as within subjects factors. The usual main effect of SOA was present for all of the ANOVAs conducted.

In the 'finger first' group, when participants were pressing the button, there was a main effect of stimulus (*F*(1,11) = 8.407, *p* = .014), indicating that RTs were significantly faster for the object (M = 387.48ms) compared to the finger (M = 419.49ms). The main effect of compatibility was approaching significance (*F*(1,11) = 4.590, *p* = .055), indicating that compatible RTs (M = 406.40ms) were faster than incompatible RTs (M = 410.35ms) **(Figure 28a)**. No other main effects or interactions were significant (*p* >.161).

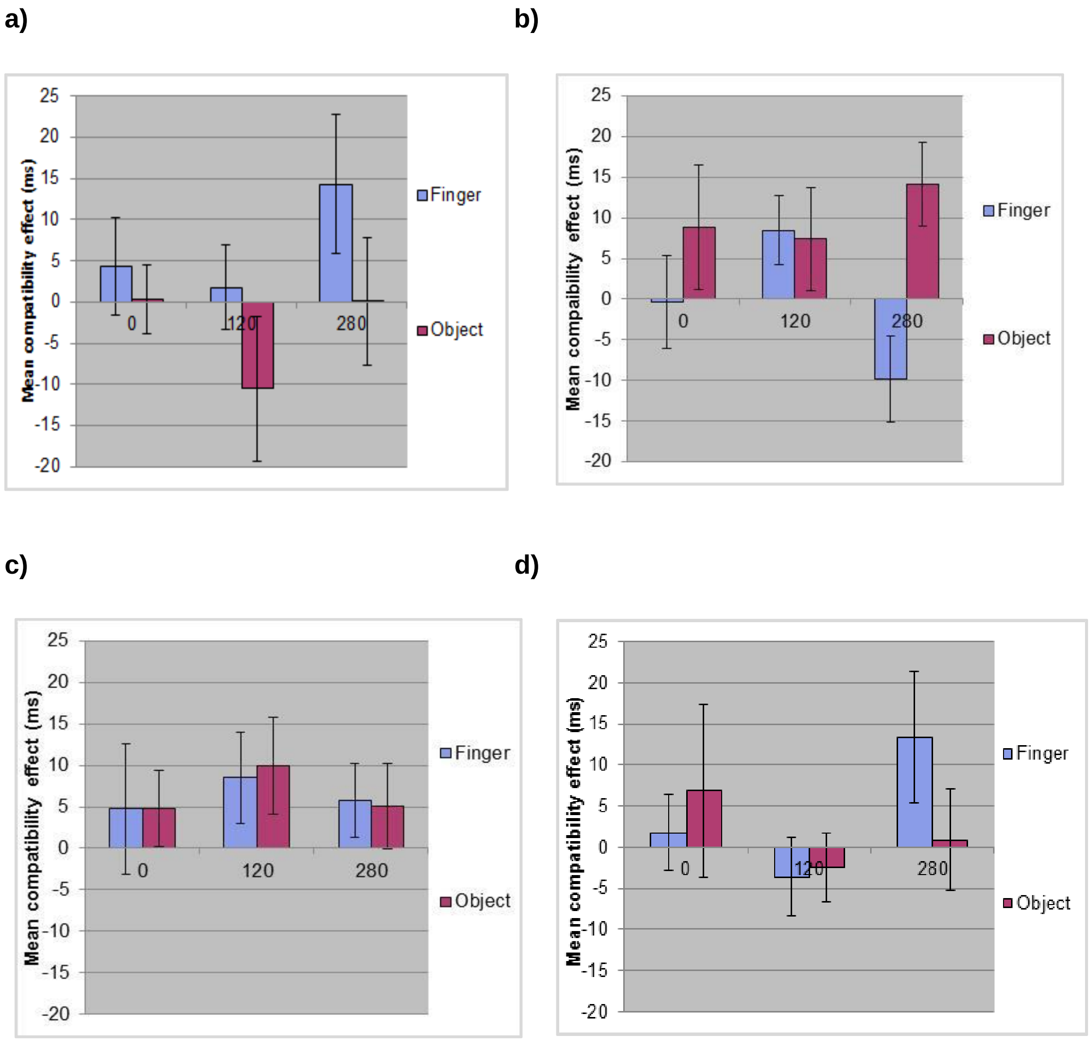


Figure 28: Compatibility effects across SOAs for the finger and object stimulus for: **a)** the finger first group (pressing responses); **b)** the finger first group (releasing responses); **c)** the object first group (pressing responses); **d)** the object first group (releasing responses).

In the 'finger first' group, when participants were releasing the button, the main effect of compatibility was approaching significance (*F*(1,11) = 3.845, *p* = .076) and there was a significant interaction between stimulus and compatibility (*F*(1,11) = 6.053, *p* = .032), indicating compatibility effects were significantly stronger for the object stimulus (M = 10.14ms) compared to the finger stimulus (M = -0.90ms) (*t*(11) = -2.460, *p* = .032) **(Figure 28b and Figure 29)**.

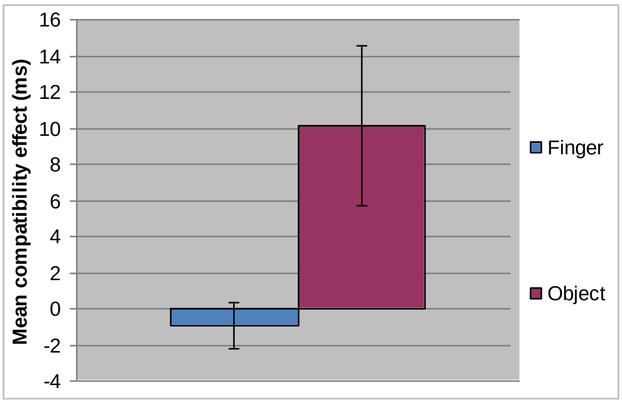


Figure 29: Figure shows the significant interaction between stimulus and compatibility in the finger first group when releasing the button.

There was also a significant interaction between view and SOA (*F*(2,22) = 8.676, *p* = .002), indicating that that the difference in RTs between the mirror and anatomical view was significantly greater at 0ms (M = 10.17ms) compared to 280ms (M = -2.24ms) (*t*(11) = -3.723, *p* = .003). Similarly, the difference in RTs between the mirror and anatomical view significantly greater at 120ms (M = 6.45ms) than at 280ms (M = -2.24) (*t*(11) = -3.546, *p* = .005). However, there was no significant difference between the mirror and anatomical view between 0 (M = 10.17ms) and 120ms (M = 6.45ms) between the mirror and anatomical views (*t*(11) = -1.156, *p* = .272). Paired t-tests also revealed that RTs were significantly faster for the mirror view (M = 308.81ms) compared to the anatomical view (M = 318.99ms) at the 0ms SOA (*t*(11) = -3.139, *p* = .009). RTs for the mirror view were also significantly faster (M = 287.24ms) than the anatomical view (M = 293.70ms) at 120ms (*t*(11) = -2.361, *p* = .038) **(Figure 30)**. There was no difference in RTs between views at 280ms (*t*(11) = .615, *p* = .551). No other main effects or interactions were significant (*p* >.115).

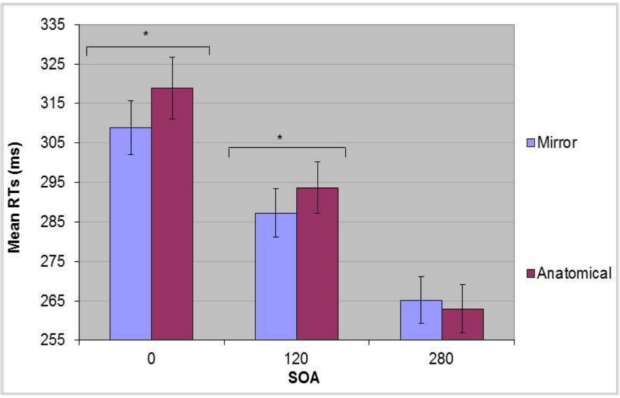


Figure 30: Figure shows the significant interaction between view and SOA in the finger first group when releasing the button. RTs were significantly faster for the mirror view compared to the anatomical view at 0ms SOA.

In the ‘object first’ group, when participants were pressing the button there was an interaction between view and SOA (*F*(2,22) = 3.752, *p* = .040), indicating that the difference in RTs between the mirror and anatomical view was significantly greater at 0ms (M = 9.08ms) compared to 120ms (M = -.79) (*t*(11) = 2.361, *p* = .038). However, the difference in RTs between the mirror and anatomical view did not differ significantly between 0ms and 280ms or between 120ms and 80ms (*p* > .096). Paired t-tests also revealed RTs were significantly faster for the anatomical view (M = 431.67ms) compared to the mirror view (M = 431.67ms) at 0ms SOA **(Figure 31)** (*t*(11) = 2.597, *p* = .025), but RTs between mirror and anatomical views did not differ at 120ms or 280ms (*p* > .184).

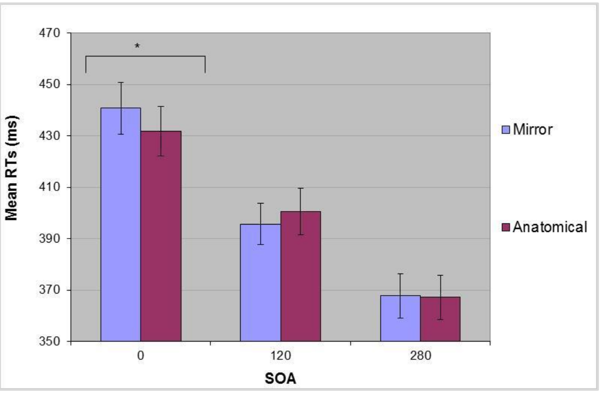


Figure 31: Figure shows the significant interaction between view and SOA in the Object First group when pressing the button. RTs for the anatomical view were significantly faster than for the mirror view at 0ms SOA.

The interaction between compatibility and stimulus was approaching significance (*F*(1,11) = 4.288, *p* = .063) indicating that compatibility effects for the finger (M = 6.81ms) were stronger than for the object (M =-3.36ms) (*t*(11) = 2.071, *p* = .063). **(Figure 32 and Figure 28c)**. No other main effects or interactions were significant (*p* >.137).

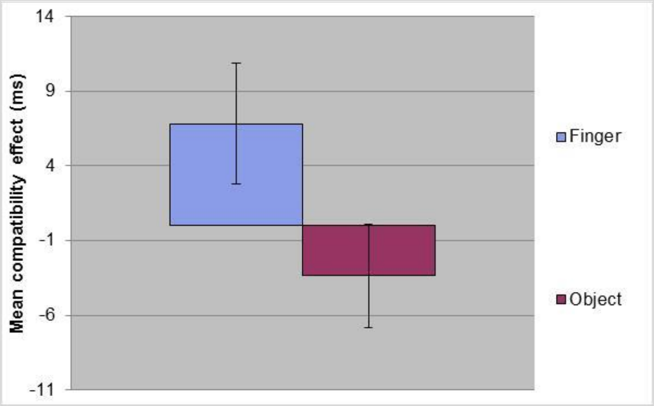


Figure 32: Borderline significant interaction between stimulus and compatibility in the object first group when pressing the button. Compatibility effects were stronger for the finger compared to the object stimulus.

Finally, in the ‘object first’ group, when participants were releasing the button the main effect of compatibility was approaching significance (F(1,11) = 4.135, p = .067), indicating compatible RTs (M = 290.08ms) were faster than incompatible RTs (M = 295.26ms) **(Figure 28d)**. However, apart from a main effect of SOA, no main effects or interactions were significant (p >.124).

2.3.2.3 Analysis of questionnaire data

Mean self-reported questionnaire scores are reported in **Table 6**. Due to the lack of imitative compatibility effects for the finger, effect of response and small group numbers no further analysis was conducted on these scores or the empathy questionnaire scores.

2.3.3 Discussion

The aim of experiment 3 was to investigate whether presenting biological and non-biological stimuli in separate blocks would modulate the level of priming produced, due to differences in attention, as opposed to mixed blocks of stimuli (experiment 1a). There were interactions with group (finger first/object first) and response type (press or release), which made the analysis of experiment 3 less clear-cut and reduced power. Although some of the results were unexpected, such as the absence of imitative compatibility effects for the finger, importantly, these results provide some suggestion that presenting stimuli in a pure block as opposed to mixed block does have an effect on imitative compatibility effects produced. In experiment 1a, where participants were presented trials in mixed blocks, we observed significantly stronger imitative compatibility for the finger stimulus compared to the object stimulus. However in the current experiment, where the stimuli were presented in pure blocks, significant compatibility effects are absent for the finger stimulus and no biological bias was present. One of the main issues with this experiment was that the power of the results described was significantly reduced due to splitting participants by starting stimulus due to order effects, thus reducing the number of participants in each group from 24 to 12. This makes it difficult to form any solid conclusions from these results alone; however, this hypothesis is explored again in experiment 4 to investigate whether the effects observed in this experiment could be replicated.

We did not expect imitative compatibility effects for the finger to be completely absent, and it is unclear why this is the case in the current study (although it seems likely that the reduced power of the experiment could explain the unusual findings). However, a finding of imitation for the object stimulus is in line with our hypothesis, as it suggests that the usual human bias observed in a mixed block scenario (experiment 1a) can be altered by reducing attention to the differences between the two stimuli, by presenting them in separate blocks. We hypothesized that imitative compatibility effects for the object stimulus to be consistent for finger first and object first groups, if the difference between experiment 1a and experiment 3 were due to reduced attention to stimulus differences. However, a compatibility effect for the object compared was only observed in the finger first condition, suggesting that the alternative hypothesis that when participants see the finger first, they may then associate the object movement they observed in the second part of the experiment with the finger movement they previously observed in the first half of the experiment may be responsible for the differences in imitative compatibility effects in the blocked condition. This interpretation is in agreement with studies which have found that the strength of imitative compatibility effects can be modulated by prior knowledge and beliefs regarding the stimulus they are observing (Liepelt and Brass, 2010; Stanley et al., 2007). Although in this experiment no explicit information or beliefs were given regarding the agency of the object, as the effect is only present in the finger first group, it is plausible that after seeing the hand stimulus initially the participants in this group created their own 'belief' that the object movement represented or was somehow associated with the hand movement they had just observed (although this may not occur on a conscious level), leading to significant compatibility effects being present for the object stimulus.

It is interesting to note that the significant interactions between view and SOA were present at 0ms SOA (releasing response). However, it is difficult to interpret why the interaction goes in opposite directions for the finger first group (where RTs were faster for the mirror view) and the object first group (where RTs were faster for the anatomical view).

2.3.4 Conclusion

In summary, we have found when we present the stimuli in pure blocks; the typical stronger imitative compatibility effects for the finger observed in experiment 1a were absent, with no imitative compatibility effects being present for the finger. Although these results have much lower power than those of experiment 1a, they do suggest that presenting the stimuli in pure blocks as opposed to in randomly intermixed blocks might have an effect on imitative compatibility effects. Importantly, experiment 1a which had an identical set up to the current experiment apart from the presentation of stimuli being in randomly intermixed blocks, as opposed to in pure blocks in the current experiment, found no imitative compatibility effects for the object. In the current experiment an imitative compatibility effect was present for the object stimulus, for the group participants who observed the hand stimulus first only. This suggests the possibility that there is a carry-over effect of seeing the hand stimulus prior to seeing the object, which may have had had an effect on the participant's implicit beliefs regarding the agency of the object stimulus, due to associating the object movement with the previously observed hand movement. This hypothesis will be explored further in **Chapter 3 (experiment 4)**.

Chapter Three

Does belief regarding stimulus agency modulate imitative compatibility effects?

3.1 Chapter Introduction

A key debate within automatic imitation research centres on whether imitative compatibility effects are actually any different from general stimulus response compatibility (SRC) effects, with some critics claiming that automatic imitation may be reducible to a 'specialized form of SRC' (Aicken et al., 2007; Jansson et al., 2007). These researchers have warned against the potential confusion of automatic imitation with spatial compatibility, and have questioned the extent to which the evidence available to date has convincingly demonstrated the existence of automatic imitation effects that are fully dissociable from spatial compatibility effects. Indeed, if the actions observed by participants are presented at locations that correspond to the location of the performed action (such as stimuli presented from a mirror view), then spatial compatibility, as opposed to automatic imitation, could explain the effects observed (Jansson et al., 2007). Furthermore, some studies showing automatic imitation for movement of non-biological stimuli has been used as evidence that automatic imitation effects actually represent SRC effects that are not specific to the imitation of biological movement.

However, in response to this criticism, a number of more recent studies have attempted to remove confounding spatial compatibility effects (Brass et al., 2001a; Gowen et al., 2010; Bertenthal et al., 2006). The difficulty in resolving this issue lies in the fact that the pattern of results predicted for imitative compatibility and all other S-R compatibility effects is identical (faster RTs for compatible relative to incompatible stimulus-response sets). Therefore, in order to conclusively disprove this claim, it is essential to use a paradigm in which the pattern of results is predicted to be different for imitative and spatial compatibility effects. As will be outlined below, a number of studies have provided evidence for the existence of a separate imitative compatibility component which can be fully-dissociated from spatial compatibility, suggesting that the two forms of compatibility effects are in fact mediated by separate cognitive processes.

In addition to presenting stimuli from an anatomical view to remove the potential confound of lateral spatial compatibility (as discussed in **section 1.6.1**), a number of different methods have been used in an attempt to dissociate imitative and spatial compatibility. For example, Bertenthal and colleagues (2006) used an effector compatibility automatic imitation paradigm in which participants were required to tap a key with either their index finger or middle finger whilst observing a video of the index finger or middle finger of a hand tapping a surface. In one condition, participants were required to imitate the cue by pressing a key with their anatomically matching finger (imitative cue). In the other condition, they were required to press a key with their spatially corresponding finger (spatial cue). However in both conditions, the other stimulus cue (although irrelevant) is also present. In experiment 1, participants observed left hand scenes, representing a mirror view with respect to the participant's right hand, and thus blending spatial compatibility and automatic imitation. In experiment 2, a separate group of participants observed right hand scenes, representing an anatomical viewpoint with respect to the participant’s right hand therefore setting spatial compatibility against automatic imitation. They argued that this may be regarded as automatic imitation as opposed to spatial compatibility; due to the fact it does not rely on activation by the stimulus movements of left-right relative position spatial codes when viewed from an anatomical view. They replicated the Brass et al. (2001a) findings in experiment 1, and observed stronger effects for the mirror view. In experiment 2, they found that the majority of the effect was due to spatial compatibility. They performed a between-experiment comparison between experiment 1 and 2, and found that the overall effect of compatibility was larger in experiment 1 compared to experiment 2, where the effects had been set in opposition, suggesting that the effects obtained in experiment 1 not entirely due to spatial compatibility i.e. automatic imitation is at least in part responsible for the observed effect. In addition, they found that while imitative compatibility effects tended to decrease significantly across a block of trials, spatial compatibility remained constant or increased slightly, suggesting they are mediated by separate processes.

However, their interpretation that the described results provide evidence of pure imitative compatibility of key tapping cannot be regarded as conclusive, due to two key issues with their methodology. Firstly, the effects obtained were using blocks in which participants were explicitly told to imitate the movement were alternated with blocks in which participants were told to imitate a symbolic cue**.** It is therefore possible that participants were affected by the inclusion of the imitative blocks, and this effect may have carried over to blocks in which a symbolic cue was used, meaning that participants may not have seen the observed movements as irrelevant to the task and continued to imitate. As argued by Catmur and Heyes (2011) the fact that they have included intertwined imitation and non-imitation blocks call into question whether the observed movements are being seen as irrelevant to the participant’s on-going task, potentially contaminating the ‘automatic’ nature of the effect. Secondly, Bertenthal et al. (2006) findings would be more convincing if the two studies had been carried out in a within context of the same experiment. The fact they have compared data between two separate groups of participant calls into question the validity of the comparisons made.

Jiménez et al. (2012; Experiment 1) recently replicated Bertenthal et al. (2006) methodology to compare performance in blocks in which stimulus were presented from a mirror orientation (left hand stimulus) and an anatomical view (right hand stimulus). They improved the experiment by using a within-participants' design and removing the explicit ‘imitation’ blocks (which potentially contaminated the automatic nature of the effect). In contrast to Bertenthal et al. (2006), they found that compatibility effect observed was equivalent for the right and left hand blocks, despite the fact they expected that the effect would be larger in the left hand block (blending spatial and imitative compatibility effects), than for the right hand blocks (setting the two effects in opposition). On this basis, they speculated that the effects observed could be attributed completely to spatial compatibility of the observed movement and response movement, and do not support the existence of imitative compatibility effects due to anatomical correspondence of the effector observed moving and the effector used to respond. They suggested that spatial compatibility effects might exert such a strong influence in the paradigm, to the point of suppressing the expression of automatic imitation effects. If this explanation is correct, one reason they may have observed such a strong influence of spatial compatibility is their use of an effector compatibility paradigm. It has been argued that the use of a movement compatibility paradigm theoretically minimizes the potential for confounding lateral spatial compatibility effects, due to the fact there is less visual processing of the stimulus occurring in order to make their response (Vogt et al., 2003). Vogt and colleagues (2003) argue that simple response tasks as opposed to effector choice response tasks provide clearer evidence for the automaticity of automatic imitation. This is because in choice response tasks participants are actively seeking further information about the required response from the visual array, whereas in a simple response task they are only required to carry out a pre specified response. However, spatial compatibility has also been shown to exert an influence in movement compatibility paradigms. For example using a movement compatibility paradigm, Gowen et al. (2010) also observed that imitative compatibility effects appear to be stronger when stimuli are presented from the mirror view as opposed to the anatomical view, supporting the theory that effects of imitative and spatial compatibility are combined in the mirror view condition, due to lateral spatial compatibility. In addition, the stronger (non-significant) compatibility effects for the mirror view in experiment 1b are likely to be caused by the enhanced influence of spatial compatibility.

Similarly, Brass and colleagues (2001a; Experiment 3) made the participant's response movement was spatially separate from the observed movement using an upside-down manipulation; in which the observed stimulus hand was in an upside-down orientation with respect to the participant's own hand **(Figure 33)**. In this experiment, for the normal hand orientation (palm down), movement direction (down) and movement type (tapping) were both compatible with a tapping response. However, for the upside down hand manipulation (palm up), movement direction was compatible to a lifting movement (up) (i.e. incompatible with tapping), while the movement type was still compatible to a tapping movement. The upside-down manipulation therefore made the movements imitatively compatible but spatially incompatible. They replicated findings of automatic imitation when participants were presented with the upside-down stimulus hand, confirming that this was due, at least in part, to correspondence of the movement type (automatic imitation), and not purely movement direction (spatial compatibility). However, the automatic imitation effect was significantly reduced in the experiment using the upside-down manipulation, in comparison to stimuli presented in the normal hand orientation (matching the orientation of the participant's own hand), suggesting a role for spatial compatibility between the participants responding hand and the stimulus in the normal hand orientation. They also conducted a distribution analysis on RTs for movement type and movement direction, and found that there was a larger increase in the compatibility effect across the RT for movement type (imitative component) than for movement direction (spatial component). This finding supports the idea that there are two separate mechanisms independently influencing the compatibility effect: a faster spatial compatibility component which shows only a very small increase over the entire distribution, and a slower imitative compatibility component which increases with time.

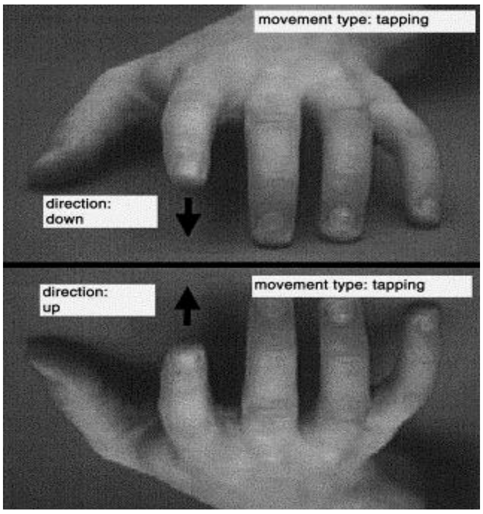


Figure 33: Stimuli used in Brass et al (2001) experiment 3.

In line with this, other groups have attempted to distinguish imitative and spatial compatibility effects based on distributional analyses of RT data. For example, Catmur and Heyes (2011) time course analysis reported that consistent with Brass et al. (2001a) findings, imitative compatibility effects increased with RT, however spatial effects did not change. These findings also indicate a dissociation in the processing of spatial and imitative compatibility, however they do not provide definitive evidence.

In addition some more recent experiments have more successfully controlled for spatial compatibility by using paradigms in which the observed stimulus movements and the participant's response movements performed in orthogonal planes, thus making the observed and executed movement spatially separate.

For example, in Press et al.'s (2008) study, they used a hand opening-closing paradigm, in which the stimulus principal axis of movement of the hand opening was mostly on a horizontal plane (left-right) whereas the response principal axis movement was mostly on a vertical plane (up-down) **(Figure 34)**. In this way, spatial compatibility and automatic imitation effects were effectively dissociated, because stimulus and response movements that were action compatible (e.g. both hands opening) were not also left-right spatially compatible.

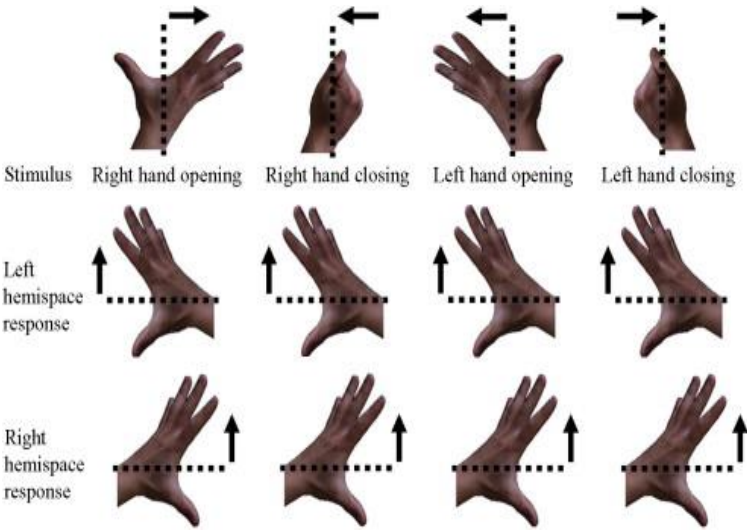


Figure 34: The design of the experiment was based on the idea that the 'principal axis of movement' of the hand opening is mostly in a horizontal plane (left-right) whereas the response principal axis movement is mostly in a vertical plane (up-down). To control for orthogonal spatial compatibility, the anatomical identity of the stimulus hand (left or right hand) was varied. The dotted line signifies the principal axis of movement, and the arrow represents the direction of finger movement (Press et al., 2008).

However, a potential issue with this orthogonal arrangement is that it may not be sufficient to control for spatial compatibility effects, due to the fact that a number of studies have identified a relatively abstract form of SRC for orthogonal stimulus and response sets where there is no 'spatial' correspondence between stimuli and responses, termed orthogonal spatial compatibility (Cho and Proctor, 2003). For example, when a stimulus is set vertically and a response set is arranged horizontally, it has been observed that an up-right/down left stimulus response mapping has an advantage over the up-left/down-right mapping (Bauer and Miller, 1982; Weeks and Proctor, 1990).

The first study to identify a statistically significant orthogonal spatial compatibility effect used a two-choice task, involving left or right movements of an index finger from a home key to a target location for which stimuli were oriented above and below a fixation point (Bauer and Miller, 1982). They observed a compatibility effect in which the above-right, below-left assignment was faster than the reverse. Such findings have been explained in terms of an extended 'salient features-coding' principle (Weeks and Proctor, 1990), arguing that S-R translation is more efficient when the S-R mapping maintains the correspondence of the salient features between the stimulus and response sets. They suggested that because in the vertical dimension, 'above' is more salient than 'below' (Chase and Clark, 1971), and in the horizontal dimension, 'right' is more salient than 'left' for right-handers (Olson and Laxar, 1973), the salient and non-salient features correspond for the up-left, down-right mapping. However, this up-right/down-left orthogonal spatial compatibility advantage has been found only when responses are made in right 'hemispace' or at body midline. The word hemispace refers to one side of space, as defined by the body midline. Complicating matters further, the effect has been shown to vary as function of response hemispace, such that when responses are made in left hemispace, the pattern is reversed with up-left / down-right mappings having the advantage (e.g. Cho & Proctor, 2004). The salient feature coding principle does not explain the fact that the effect has been shown to change as a function of response hemisphere, and hand posture (e.g. Michaels, 1989; Weeks et al., 1995), therefore more recent accounts have attributed orthogonal spatial compatibility to ‘coding asymmetry’ (Cho and Proctor, 2001; Lippa and Adam, 2001; Weeks and Proctor, 1990). According to the ‘multiple asymmetric codes’ account, stimulus and response alternatives are coded asymmetrically; therefore, since up/right and down/left are the salient polar referents for their respective spatial dimensions, stimulus response translation is faster when the salience of the response set corresponds to that of the response set (Cho and Proctor, 2003).

Therefore, Press et al. (2008) also controlled for the ‘orthogonal spatial compatibility effects’ described by Weeks and Proctor (1990) by varying anatomical identity of the stimulus hand (left or right hand) and the response hemispace (left or right). As it had been previously observed (Cho and Proctor, 2004) that orthogonal spatial compatibility effects affected by response hemispace, but are not affected by response hand; participants used their left hand to respond in the right hemispace and their right hand to respond in the left hemispace **(Figure 35)**. They predicted that if both automatic imitation and orthogonal spatial compatibility contribute to the compatibility effect, the effect would be greater with the right stimulus hand compared to the left stimulus hand. Using this method, they were able to isolate automatic imitation and spatial compatibility, while controlling for orthogonal spatial compatibility. They observed that action compatible responding was faster than action incompatible responding for both left and right hand stimuli, indicating the presence of imitative effect that could not be accounted for by spatial compatibility. In addition, the fact that the effect was present regardless of whether the observed movement was a left or right hand suggests performance was not influenced by orthogonal spatial compatibility.

However, Jiménez et al. (2012) argue that since Press and colleagues (2008) task required the participant to produce a more complicated response that was composed of more than one element (i.e. the opening or closing a clenched fist depends on the way that the spatial relationship between the palm, thumb and fingers change over time, by moving these parts towards or away from each other) that it could be argued that spatial compatibility should be defined in terms of the spatial relations established between the separate components of the action as opposed to the ‘absolute spatial coordinates’. They therefore suggest it is possible compatibility effects could have arisen due to relative directional spatial compatibility effects of each of the components of the movement as opposed to imitative compatibility effects. The fact that in using the same hand stimulus with a ‘robotic control’ hand (controlled for size/luminance) and schematic hands, Press et al (2005) found imitation for the robotic stimuli (to a lesser extent) also indicates the possibility the effects found arose from either relative or absolute spatial compatibility effects i.e. spatial compatibility may have been greater for the hand due to the relative compatibility of the direction of movement of the separate components (fingers/thumb), as opposed to the overall directional compatibility of the movement (opening and closing) of the robotic stimuli (which lacked the spatial compatibility of the separate components of individual fingers). In addition, it could be argued that the observed stimulus movement was not clear-cut movement to the left or right (since the fingers move in the opposite direction to the thumb for opening, and both thumb and fingers towards the palm for closing). For the same reason it could be argued that the participant's response movement hand is not a clear cut up-down movement. This could explain why no orthogonal compatibility effects were observed.

Two groups have recently used rotated scenes and have observed the presence of imitative compatibility effects in the absence of confounding spatial compatibility effects using key pressing effector compatibility paradigms. In the first group, imitative compatibility effects were present using a rotated effector compatibility paradigm (Cook and Bird, 2011, 2012). However, in this paradigm imitative compatibility was potentially confounded with orthogonal spatial compatibility effects. This is because hand was rotated such that the middle finger was located on an upper portion of the screen relative to the index finger on the lower portion of the screen. Based on the U-R, D-L mapping advantage, the observed middle finger movement (up) would be orthogonally compatible with a response on the right (middle finger of right hand is spatially on the right) and the observed index finger movement (down) would have an advantage to the left (participant's index finger of right hand is spatially to the left) **(Figure 35)**. In addition, Jiménez et al. (2012) contend that since the authors additionally found similar effects when the effector was highlighted with a colour change (but no movement occurred) **(Figure 46)**, while the authors suggest this was caused by an 'effector priming effect', it could be argued that the fact that the effect was also present in the absence of movement might indicate the effects observed might be due to the influence of orthogonal spatial compatibility.

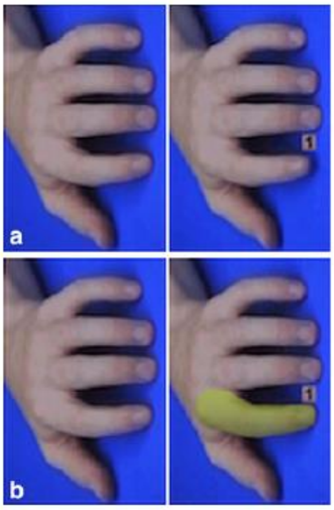


Figure 35: Imitative compatibility is potentially confounded with orthogonal spatial compatibility (up-right, down-left) advantage (Cook and Bird, 2012).

However, the second group also controlled for orthogonal spatial compatibility effects (Jiménez et al., 2012; Experiment 2). In this study, participants observed rotated scenes of an index or middle finger movement, and responded with a key press using either the index or middle finger; thus the observed images were on an orthogonal plane (upper and lower hemi-field) with respect to the observer's response action (right or left) **(Figure 37)**. Importantly, as in Press et al. (2008) they varied the anatomical identity of the observed hand to control for orthogonal spatial compatibility effects. They found that automatic imitation effects were consistently found, showing faster RTs when the observed effector was compatible with the response effector, indicating the effects are dissociable. In addition, as in Press et al. (2008), the effect was present regardless of whether the response movements were produced by a right or left hand (suggesting a lack of influence of orthogonal spatial compatibility).

In summary, while on the surface automatic imitation appears to share common features with the more general framework of SRC effects; there is now a great deal of evidence indicating that automatic imitation is an independent and dissociable effect. Recently, the term 'imitative compatibility' has been introduced by some scholars (Boyer et al., 2012; Catmur and Heyes, 2011) to refer to automatic imitation effects which have been 'cleaned' from spatial compatibility effects.

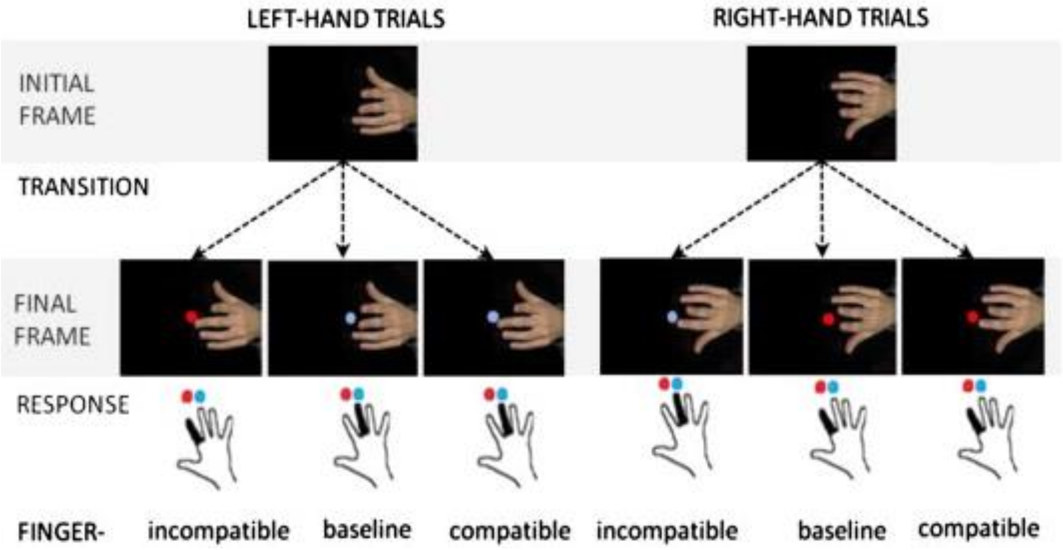


Figure 36: Jiménez et al. (2012, Experiment 2) rotated key pressing paradigm.

In **Chapter 3** we have modified the original movement compatibility paradigm used in Chapter 2, in order to remove any non-specific spatial SRC effects, and isolate the imitative component. The experiments in Chapter 3 use a shorter rotated version of the original experimental paradigm used in Chapter 2, in which images were presented in an orthogonal arrangement with respect to the observer's response, thus allowing us to separate spatial compatibility and automatic imitation effects. We have also controlled for orthogonal spatial compatibility effects by effectively pitting imitative compatibility against orthogonal spatial compatibility. The primary aim of **experiment 4** was to initially evaluate the new paradigm, assessing whether 1) significant imitative compatibility effects would be present using the rotated paradigm (where lateral spatial compatibility is removed) and imitative compatibility is pitted against orthogonal spatial compatibility, 2) a significant difference between imitation for the finger and object stimulus would be still present in the mixed condition, and 3) whether significant orthogonal compatibility effects would be produced. Additionally, we further investigated the effects of presenting biological and non-biological stimuli in mixed vs. pure blocks.

In **experiment 5** and **experiment 6**, we continued to use the rotated automatic imitation paradigm. We aimed to further investigate whether manipulating participant's belief regarding the agency of the object stimulus (by informing participants that the object movement was generated from a human finger movement) would modulate automatic imitation, leading to stronger automatic imitation effects for the object stimulus relative to when no information was given regarding the origin of the object stimulus. This would provide convincing evidence that automatic imitation can be modulated by top-down factors, such as beliefs regarding stimulus agency. The idea that prior knowledge regarding biological origin might modulate imitative compatibility effects is described in detail in **section 1.7.1** and **section 3.2**.

3.1.1 Experiment 4 - Introduction

In experiment 4, the observed stimulus images were rotated 90 degrees counter-clockwise, while participants as normal by pressing or releasing a key. This arrangement makes the movement direction of the stimulus on the screen (left-right) orthogonal to the participant's response direction (up-down). In this orientation, a rightward movement represents a finger depression (imitatively compatible with a press response for the hand stimulus). However a rightward movement is orthogonally compatible with a release response (up/right mapping advantage) for the object stimulus. Conversely, a leftward movement is imitatively compatible with releasing for the hand stimulus, but orthogonally compatible with pressing for the object stimulus **(Figure 37a and 37b).**

There are two main advantages to using this 'neater' rotated version of paradigm. Firstly, this version of paradigm removes the confound of lateral spatial compatibility, thus giving a purer measure of imitative compatibility effects (represented by positive compatibility effects). On a similar note, this arrangement removes the necessity to present the two viewpoints (mirror and anatomical) creating a quicker and more succinct experiment and reducing complexity when analysing the data. Secondly, this rotated paradigm also potentially allows for the measurement of orthogonal spatial compatibility effects (which would be represented by reverse imitative (negative) compatibility effects).

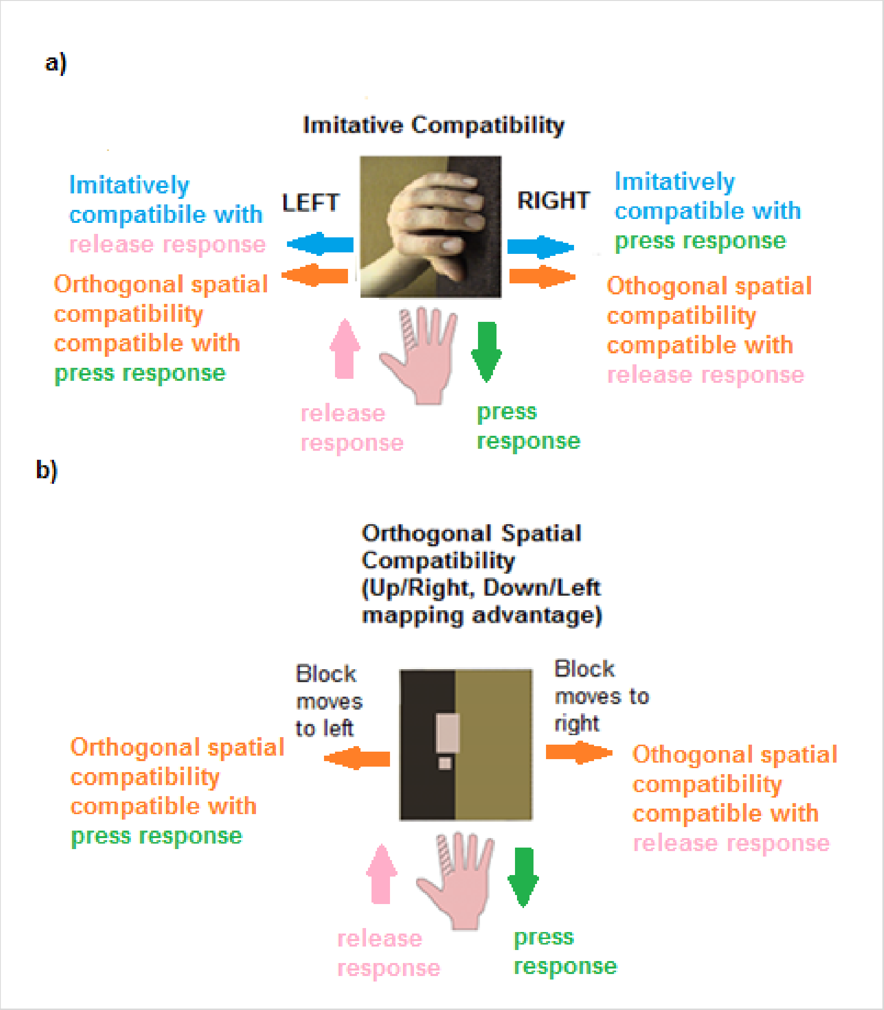


Figure 37: Imitative compatibility effects are effectively being pitted against orthogonal spatial compatibility effects in this rotated paradigm.

The primary aim of experiment 4 was to create a neater version of our movement compatibility paradigm which removes lateral spatial compatibility, while dissociating imitative compatibility effects from orthogonal compatibility effects.

The secondary aim was to further investigating the effect of presenting the stimuli in pure blocks or randomly intermixed blocks; and in the pure blocks if the order in which the stimuli are presented has an effect on the magnitude of automatic imitation. In the 'mixed' group (based on the results of experiment 1a), we predicted that the greater imitative compatibility effects would be present relative to the object stimulus. However, due to the changes made, an alternative possibility would be that imitative compatibility would be present for the hand stimulus while orthogonal spatial compatibility would be present for the object stimulus. In the 'blocked' group, we had separate hypotheses for the finger first vs. object first groups. In the finger first group we predicted that imitative compatibility would be present for object stimulus, if the previously observed effect for the object in the 'finger first' group in experiment 3 was a true effect caused by participants creating their own belief that the object stimulus movement is associated with the previously observed human hand movement.

3.1.2 Methods

3.1.2.1 Participants

48 right-handed healthy individuals (23 female), with a mean (±SD) age of 23.25 (± 4.5) years were recruited. The mean laterality quotient was 83.12 (SD = 19.14). The study consisted of a single testing session lasting approximately 1 hour, and participants were paid £5 for their participation.

3.1.2.2 Stimuli

The finger and object stimulus images used were identical to those used in experiment 1 **(section 2.2.2)**. However, the images were rotated 90 degrees counter-clockwise **(Figure 37 and Appendix C2 and C3)**. The series of rotated images for both stimuli were presented in quick succession. As the images were rotated a leftward movement represented a finger lift (compatible with a button release response) and a rightward movement represented a finger depression (compatible with a button press response). Due to the fact the object is rotated, it should not be associated with an upward or downward movement; but gives the impression of leftward or rightward movement. The experimental setup was identical to that of experiment 1a. Participants were required to complete the ELI questionnaire for handedness.

3.1.2.3 Design and procedure

Participants performed the same task as described in experiments 1a and 1b. The participants were split into two groups: a mixed group (n= 24) and a blocked group (n = 24). In the mixed group, participants observed the finger movement trials and object movement trials randomly mixed within the same block of trials. In the blocked group, participants observed only the finger movement trials or only object movement trials within a block of trials. Halfway through the experiment, the stimulus was switched to the stimulus they had not already observed in the first half. Half of the blocked group participants (n=12) viewed the finger movement trials only first, and half of the participants (n = 12) viewed the object movements first.

The experiment consisted of a total of 384 trials. All participants completed 8 practice trials (8 go/8 no-go) at the start of the experiment and each time the response was changed between pressing and releasing responses, giving a total of 48 practice trials throughout the experiment. A short rest period was given every 48 trials, and a longer break was given half way through after 192 trials. During the first 2 blocks of 48 trials, participants in both groups carried out a pre-specified response of either pressing or releasing the button for 96 trials. The response was then switched to the opposite response for 2 blocks of 48 (96) trials. Halfway through participants switched back to the starting responses for 96 trials, then again switched to the opposite response for the final 96 trials. The starting response was counterbalanced across participants in both groups.

In the blocked group, the trials were split by stimulus type. For each stimulus block, there were therefore 6 experimental conditions (compatibility (2) x SOA (3) = 6) which were each presented 24 times (6 x 24 = 144); in addition 24 baseline trials and 24 no-go trials were added making up the total of 192 trials for each stimulus (144+24+24 = 192 trials) 192/4 = 48. The 192 trials for the object stimulus plus 192 trials for the finger stimulus, presented in separate blocks, make up the total of 384 trials.

In the mixed group trials were randomly intermixed, therefore there were 12 experimental conditions (stimulus (2) x compatibility (2) x SOA (3). Each experimental condition was presented 24 times (12 x 24 = 288); in addition 48 baseline trials and 48 no-go trials were included, making the total of 288+48+48 =384 trials. All stimulus conditions were presented randomly within each block.

3.1.3 Results

3.1.3.1 Analysis of error data

The same exclusion criterion used in the previous experiments was applied **(section 2.1.3.1).** This resulted in a total loss of 2.29% of trials on average from the mixed group and 2.54% of trials on average from the blocked group. In addition, the same error types (described in experiment 1a) could be incurred in this experiment.

Overall, participants in both the mixed and blocked group made a low level of errors **(Table 11 and Table 12)**; therefore no individual participant's data was removed from the study. The error participants were most prone to was the no-go error.

Table 11: Mean (±SE) % errors calculated as a percentage of the total number of trials where the error could occur for each type of error.

Type of Error (total number of trials where error could occur)	Experiment 4 - Mixed Group	Experiment 4 - Blocked Group
Anticipation error (336)	1.07 (± 0.32)	0.67 (± 0.21)
No-go Error (48)	8.42 (± 1.78)	5.83 (± 1.23)
Second response error (384)	0.15 (± 0.11)	0.01 (± 0.01)

Table 12: Mean % no-go and anticipation errors (± SE) for each stimulus. No-go errors were made out of a potential 48 and anticipation errors were made out of a potential 336. **Bold** type represents compatible trials.

Stimulus	Group	Mean % No-go errors (± SE)	Mean % Anticipation errors (± SE)
Finger	Mixed	**2.26 (±0.32)** 2.60 (± 0.30)	**0.05 (± 0.05)** 0.07 (± 0.06)
	Blocked	**2.00 (± 0.35)** 1.74 (± 0.17)	**0.03 (± 0.04)** 0.02 (± 0.02)
Object	Mixed	**1.56 (±0.20)** 2.00 (± 0.27)	**0.04 (± 0.05)** 0.04 (± 0.04)
	Blocked	**0.78 (± 0.15)** 1.30 (± 0.15)	**0.04 (± 0.02)** 0.04 (± 0.04)

3.1.3.2 Analysis of reaction time data

Overall mean RTs (ms) (±SE) are presented in **Table 13**. Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects.

Table 13: Mean RTs (ms) (±SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (*p* < .05).

Stimulus	Response	SOA	Mean RT in Mixed (ms) ± SE	Mean RT in Blocked (ms)+ SE
Finger	Press	0	**308.91 (± 13.72)** 305.00 (± 13.24)	**316.83 (± 11.55)** 306.57 (± 10.73)
		120	**289.05 (± 11.67)** 282.91 (± 13.31)	**278.70 (± 9.77)** 293.43 (± 10.38)*
		280	**256.62 (± 11.98)** 271.58 (± 10.59)*	**255.37 (± 8.63)** 265.32 (± 8.61)* *p =.056*
	Release	0	**318.73 (± 13.31)** 318.83 (± 13.67)	**318.56 (± 9.37)** 319.03 (± 9.45)
		120	**287.68 (± 10.51)** 294.09 (± 10.32)*	**284.26 (± 8.17)** 279.39 (± 7.76)*
		280	**275.96 (± 9.06)** 264.42 (± 9.89)* *p=.060*	**278.04 (± 7.33)** 274.29 (± 8.25)
Object	Press	0	**328.91 (± 17.21)** 322.75 (± 15.64)	**311.22 (± 11.05)** 305.30 (± 10.78)
		120	**290.28 (± 13.43)** 295.14 (± 13.51)	**278.77 (± 7.97)** 282.54 (± 9.65)
		280	**265.89 (± 13.50)** 272.90 (± 12.61)	**249.48 (± 9.20)** 249.61 (± 8.47)
	Release	1600	**328.89 (± 13.16)** 320.00 (± 14.34)	**308.44 (± 7.31)** 312.84 (± 8.71)
		120	**296.65 (± 13.05)** 298.23 (± 10.36)	**289.36 (± 7.61)** 285.99 (± 7.86)
		280	**267.66 (± 9.58)** 269.16 (± 11.73)	**259.68 (± 6.78)** 264.92 (± 7.54)* *p = .056*

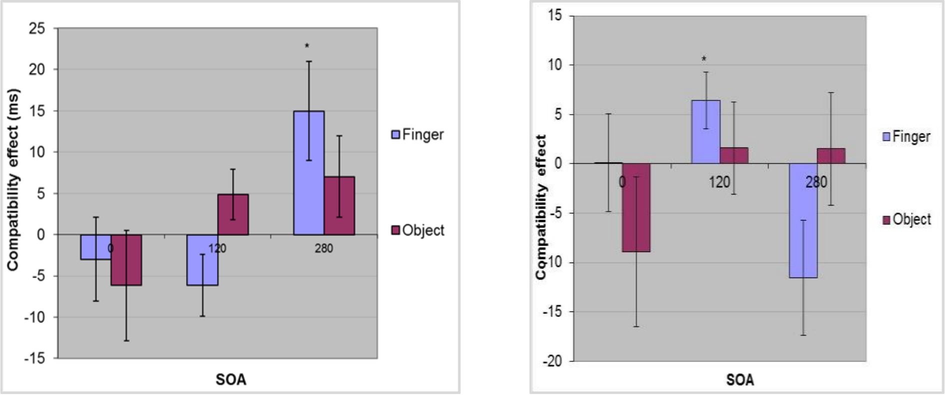
Two initial mixed design repeated measures ANOVAs for each group (mixed and blocked) were conducted on participant's mean RTs; with response type (press/release) x stimulus (hand/object) x compatibility (compatible/incompatible) x SOA (0, 120, 280) as within-subjects factors. In the mixed group, there was a borderline significant main effect of response type for the mixed group (*F*(1,23) = 3.972, *p* = .058) and a number of significant interactions with response type, including an interaction between response, stimulus, SOA and compatibility (*F*(2,46) = 5.245, *p* = .009), and a borderline significant interaction with response type in the blocked group. Due to the significant interactions with this factor, mean RTs across press and release were analysed separately for press and release responses for both groups.

Four within-participant ANOVAs (mixed (press), mixed (release), blocked (press), blocked (release)) were conducted on participants' mean RTs with stimulus (hand/object) x compatibility (compatible/incompatible) x SOA (0, 120, 280) as within-subject factors. The usual main effect of SOA was present for all of the ANOVAs.

3.1.3.2.1 Mixed group

An ANOVA for pressing responses revealed there was a main effect of stimulus (*F*(1,23) = 12.233, *p* = .002) indicating that RTs were significantly faster for the finger (M = 280.58ms) compared to the object (M = 290.02ms). There was also a significant interaction between compatibility and SOA (*F*(2,46) = 4.574, *p* = .015) and a significant interaction between stimulus and compatibility and SOA (*F*(2,46) = 3.868, *p* = .028) indicating that compatibility effects were significantly stronger for the finger (M = 16.74ms) compared to the object stimulus (M = 4.89ms) at 280ms (*t*(23) = 2.300, *p* = .031), but compatibility effects between the finger and object did not differ significantly at 0ms or 120ms (p >.093) **(Figure 38a)**. No other significant main effects or interactions were significant (*p* >.076).

An ANOVA for releasing responses only revealed the usual significant main effect of SOA **(Figure 38b)**. No other significant main effects or interactions were significant (*p* >.086).



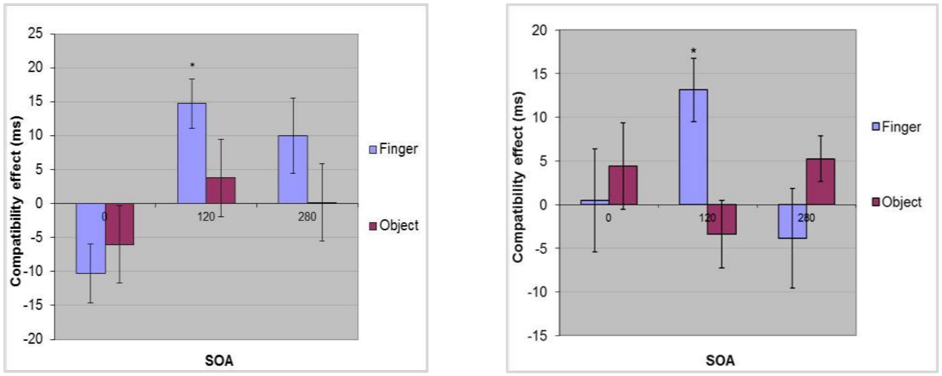
a) **b)**

Figure 38: Mixed group: a) for pressing responses; b) for releasing responses.

3.1.3.2.2 Blocked group

An ANOVA for pressing responses revealed that there was a significant interaction between compatibility and SOA (*F*(2,46) = 6.815, *p* = .003), indicating RTs were significantly faster for compatible trials (M = 282.96ms) compared to incompatible RTs (M = 292.94ms) at 120ms (*t*(23) = -3.831, *p* = .001) **(Figure 39a)**, but not at 0ms or 280ms (*p* >.105). The interaction between stimulus and compatibility was approaching significance (*F*(1,23) = 4.098, *p* = .055) indicating the compatibility effects for the finger (M = 7.09ms) were significantly stronger than for the object stimulus (M = -1.02ms) (*t*(23) = 2.024, *p* = .055).

An ANOVA for releasing responses revealed that there was a main effect of stimulus (*F*(1,11) = 6.304, *p* = .020) indicating that responses were significantly slower for the finger (M = 292.63ms) compared to the object stimulus (M = 285.84ms). There was also a significant interaction between stimulus, compatibility and SOA (*F*(2,46) = 4.614, *p* = .015) indicating that compatibility effects were significantly stronger for the finger stimulus (M = 13.13ms) compared to the object stimulus (M = -3.37ms) at 120ms (*t*(23) = 2.714, *p* = .012), but did not differ significantly at 0ms or 280ms **(Figure 39b)**.



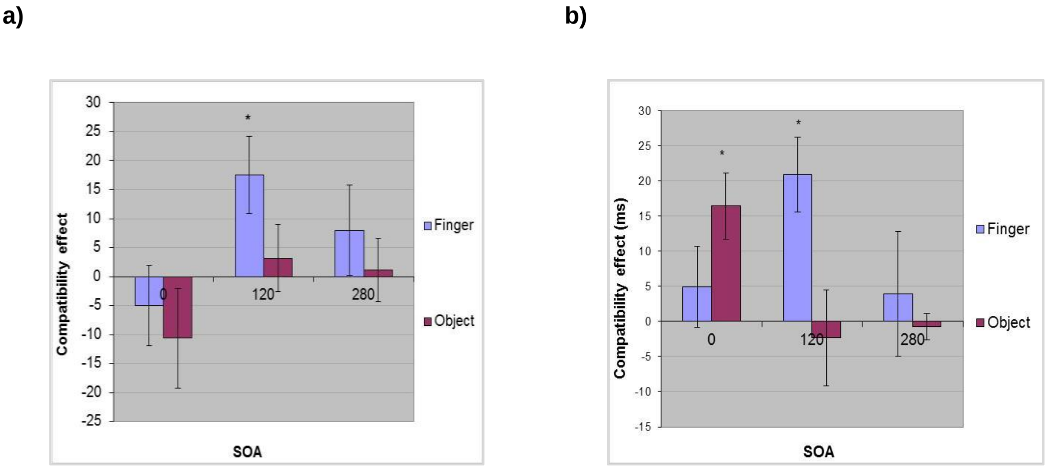
a) **b)**

Figure 39: Blocked group: a) pressing responses; b) releasing responses.

In order to investigate whether any the order effect would be present due to seeing the finger first compared to seeing object first a separate ANOVA was carried out with response x stimulus x compatibility x SOA as within subjects factors, and group (finger first v object first) as a between subjects factor revealed a significant five-way interaction between response, stimulus, compatibility, SOA and group (F(2,44) = 3.256, p = 0.046). Due to this interaction with response and group, and in order to simplify this five-way interaction, four additional ANOVA's were carried out; 2 ANOVAs for pressing responses with a separate ANOVA for each group (finger first group/object first group), and 2 ANOVAs for releasing responses (with a separate ANOVA for each group); with view, stimulus, compatibility and SOA as within subjects factors. The usual main effect of SOA was present for all of the ANOVAs conducted.

In the finger first group, when participants were pressing the button, there was a significant interaction between compatibility and SOA (*F*(2,22) = 4.412, *p* = .024), indicating compatibility effects were significantly stronger at 120ms (M = 10.37ms) compared to 0ms (M = -7.80ms) (*t*(11)= -2.950, *p* = .013) **(Figure 40a)**. There was a large compatibility effect present for the finger stimulus at 120ms; however the interaction between compatibility, stimulus and SOA was not significant (*F*(2,22) = .304, *p* = .741).

In the finger first group, when participants were releasing the button there was a main effect of stimulus (*F*(1,11) = 13.949, *p* = .003) indicating participants responded significantly faster to the object stimulus (M = 298.99ms) compared to the finger stimulus (M = 304.01ms). There was a main effect of compatibility (*F*(1,11) = 12.040, *p* = .004), which indicated that participants' RTs were significantly faster for compatible (M = 293.98ms) compared to incompatible (M = 300.03ms) trials. There was also a significant three way interaction between stimulus, compatibility and SOA (*F*(2,22) = 5.072, *p* = .015) indicating that compatibility effects were stronger for the finger (M = 18.78ms) than for the object (M = -2.15ms) at 120ms and this difference was approaching significance (*t*(11) = 2.121, *p* = .057) **(Figure 40b)**. Paired t-tests also revealed that for the finger stimulus compatibility effects were significantly stronger at 120ms (M = 18.78ms) compared to 0ms (M = -2.03ms), and the difference between compatibility effects at 120ms (M = 18.78ms) and 280ms (M = .90ms) was approaching significance. For the object stimulus compatibility effects were significantly stronger at 0ms (M = 17.31ms) compared to 120ms (M = -2.14ms), and at 0ms (M = 17.31ms) compared to 280ms (M = 3.51ms).



a) **b)**

Figure 40: Blocked finger first group: a) pressing responses; b) releasing responses.

In the object first group, when participants were pressing the button, there was a large compatibility effect for the finger stimulus at 120ms; however there was not a significant interaction between stimulus, compatibility or SOA (*F*(1,11) = 1.318, *p* = .275) **(Figure 41a).** Apart from a main effect of SOA, no other main effects or interactions were significant.

When participants were releasing the button in the object first group, there was a significant three-way interaction between stimulus, compatibility and SOA (*F*(2,22) = 4.236, *p* = .028). Paired t-tests show that compatibility effects were stronger for the finger than for the object at 120ms (*t*(11) = 1.649, *p* = .127), while the compatibility effects for object were stronger than for the finger at 280ms (*t*(11) = -1.689, *p* = .119); however these differences did not reach significance **(Figure 41b)**. Apart from a main effect of SOA, no other main effects or interactions were significant.

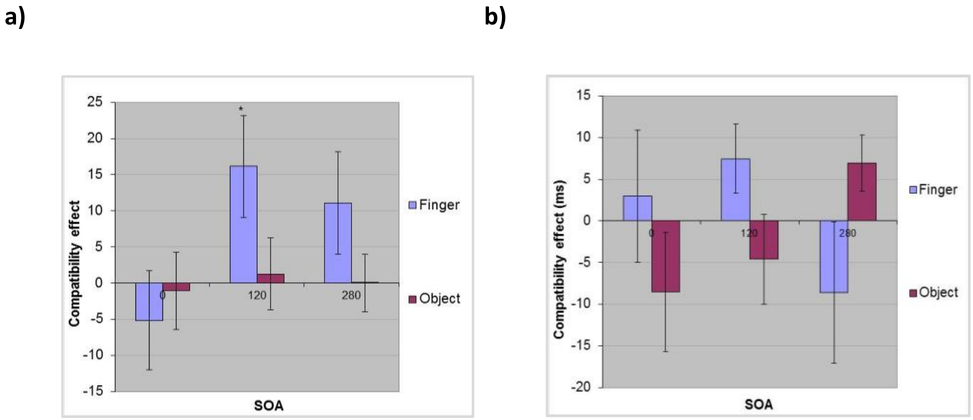


Figure 41: Blocked object first group: a) pressing responses; b) releasing responses.

3.1.4 Discussion

Experiment 4 has produced four main findings of interest. Firstly, we aimed to create a neater version of our movement compatibility paradigm in which imitative compatibility effects could be isolated from lateral spatial compatibility effects. In this respect, the experiment was successful as automatic imitation effects were present, despite the orthogonal spatial compatibility being pitted against automatic imitation. Secondly, it is interesting to note that no significant influence of orthogonal spatial compatibility was found. Thirdly in the mixed group, we have replicated findings of significant automatic imitation for the finger; however no imitative compatibility or orthogonal spatial compatibility effects were present for the object stimulus. Finally, in the blocked group, consistent with experiment 3, compatibility effects for the object stimulus were only present in the ‘finger first’ group. However, although we predicted orthogonal compatibility effects would be produced for the object in the object first group; no significant orthogonal compatibility effects were observed. These findings will be discussed in turn.

3.1.4.1 Automatic imitation present using rotated paradigm

Firstly, using the rotated version of paradigm, we have found that significant automatic imitation effects were present in a situation where confounding spatial variables have been removed, and imitative compatibility is potentially pitted against orthogonal spatial compatibility. This is a significant finding since as discussed; some groups have questioned whether imitative compatibility effects are distinct from other forms of SRC (Aicken et al., 2007; Jansson et al., 2007). The current study provides convincing evidence of the existence of a separate imitative compatibility effect that is not reducible to spatial compatibility effects. This finding is compatible with evidence suggesting that the processes mediating imitative compatibility effects are distinct from the processes mediating spatial compatibility (Catmur and Heyes, 2011; Brass et al., 2001a). It is also in line with studies using similar methods of setting the stimuli in an orthogonal arrangement relative to the participant’s response, and found an imitative compatibility component that is distinct from spatial compatibility effects (Press et al., 2008, Jiménez et al., 2012, Experiment 2).

3.1.4.2 Absence of orthogonal spatial compatibility effects

As discussed, the rotated paradigm also potentially allows for the measurement of the strength of orthogonal spatial compatibility effects. We expected that imitative compatibility effects should not be produced for the object stimulus in the current paradigm, as due to rotating the stimuli, the object movement should be associated with left/right movement (as opposed to up-down movement of the finger). In particular, we hypothesized that in the ‘object first group’ where the hand stimulus has never been observed no imitative compatibility should be produced. As predicted, imitative compatibility effects for the object are absent in the object first group. We also predicted that an up-right/down-left orthogonal spatial compatibility advantage might be present for the object stimulus, particularly in the ‘object first’ group of participants, as the object should be associated with a left-right movement, and the response would be associated with an up-down movement. However, there was no evidence of orthogonal compatibility effects affecting performance in our rotated version of the paradigm for either stimulus in any of the conditions. This is in line with the findings of previous groups using similar methodologies to that of the current experiment in which orthogonal compatibility effects were reportedly absent (Press et al., 2008; Jiménez et al., 2012, Experiment 2).

One possibility is that the orthogonal compatibility effect is a weak overall effect, thus does not influence performance in the current version of the paradigm. This may be due to differences in the current experimental set up in comparison with the studies that originally identified the effect. For example, one key difference which may account for the lack of orthogonal compatibility effects being present in this experiment could be that our ‘up/down’ in the current experiment refers to a vertical pressing (down) or releasing (up) response which is spatially in the same place, using a key in the same spatial location to make the response, as opposed to using two separate keys, which are physically above and below a central ‘home’ key. For example, in the original experiments reporting the up-right, down-left advantage, the stimuli were set vertically (appeared either above or below a fixation point on the screen), and the participants participated in a two choice task, involving either toggles a switch left or right from a neutral position or make right or left movements of their finger from a home key to a target key (Bauer and Miller, 1982; Michaels, 1989; Weeks et al., 1995) **(Figure 43a)**. Moreover, studies which have found the orthogonal compatibility effect for key pressing responses, have involved left or right movements of an index finger of one hand from a home key to a target location (Bauer and Miller, 1982; Weeks and Proctor, 1990) or bilateral pressing of keys with left index finger pressing the left key, and right index finger pressing the right key **(Figure 43b)**. This clearly differs from the current arrangement, as there is no physical movement of the hand during key pressing or releasing responses.

Lippa (1996) proposed a referential coding hypothesis to explain the orthogonal SRC effects obtained with unilateral movement response. The hypothesis suggests that orthogonal SRC is a SRC effect similar to that which occurs with parallel stimulus and response orientations. Based on idea that coding can occur with respect to various frames of reference, Lippa proposed that when unilateral responses were made, response locations are coded spatially in reference to the intrinsic axis from the fingertip to the wrist to bring them in line with the stimulus locations. Lippa argues that when participants make unilateral up down responses to stimuli in left right locations, because no specific instructions are given about hand posture, participants typically hold their arm/hand in naturally comfortable posture at angle of approximately 45-90 degrees relative to the line of the response keys. If the hand (intrinsic fingertip-to-wrist axis) functions as a reference point defining the position of the response keys, everything located to the left of the hand may be coded as left, and everything located to the right may be coded as right. Thus due to the hand posture when responding with the right hand, the upper key (on right side of responding hand) would be coded as right and the lower key would be coded as left. Conversely, with left hand responding, the upper key would be coded as left and the lower key would be coded as right.

Importantly, if this explanation for orthogonal compatibility effects is correct, for unilateral key presses using the right hand, this U-R/D-L advantage would only been found in paradigms in which the response key is physically above or below, as only physically upwards and downward responses would be coded as left/right responses. In the current experiment there is no physical movement between spatially distinct locations above or below, as the participant is simply pressing or releasing one key in one location, therefore it would make sense that orthogonal compatibility effects would be absent.

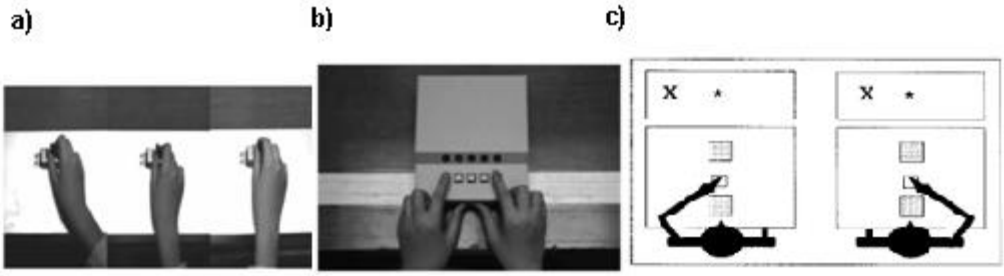


Figure 42: Example of typical responses in original orthogonal spatial compatibility paradigms: **a)** unilateral switch toggle response from left to right (taken from Cho et al., 2008); **b)** bilateral left or right button press (taken from Cho et al., 2008) **c)** unilateral pressing of keys above or below a central home key, with the hand in a natural comfortable position at a 45-90 degree angle to the key (Experiment 1; Lippa et al., 1996).

In addition, another a key difference in the design of studies in which orthogonal compatibility has been found is the sudden onset of the target stimulus (such as an X or coloured LED target) relative to a fixation point, rather than stimulus which is displayed on the screen for a number of seconds before movement from one location on the screen to another occurs, as in the current experiment. Together, these differences may have contributed to the absence of significant orthogonal compatibility effects for the object stimulus (particularly in the object first group).

3.1.4.2 Mixed vs blocked group findings

We hypothesized that in the mixed group stronger imitative compatibility effects would be present for the hand stimulus relative to the object stimulus. In line with our predictions, in the mixed group, we found imitative compatibility effects for the finger stimulus; however no significant imitative (or orthogonal spatial compatibility) effects for the object. This replicates our previous findings in experiment 1a, where imitative compatibility effects were present for the finger stimulus but not for the object stimulus. The absence of imitative compatibility effects for the object stimulus in the mixed group are compatible with the hypothesis proposed by Gowen and Poliakoff (2012). This hypothesis suggests that in the mixed condition, attention is drawn to stimulus differences, leading to a modulation in imitative compatibility effects such that responses for the object stimulus are actively inhibited via the top-down modulation route described in **section 1.8**, resulting in a loss of the compatibility effect for the object. Conversely, reduced inhibition of the compatibility effects for the object may occur when the object is presented in separate blocks, as less attention is drawn to stimulus differences when stimuli are presented in separate blocks of trials. However, an alternative explanation for the emergence of compatibility effects in the blocked condition is suggested by the results of experiment 3, where we observed an imitative compatibility effect for the object in the ‘finger first’ group only. We interpreted this such that participants were creating their own belief that the object movement represented the initially observed finger movement in the finger first group.

The current experiment replicates the findings of experiment 3, as we have found a significant imitative compatibility effect for object was only present in the ‘finger first’ group. For the object first group, we expected orthogonal spatial compatibility as opposed to imitative compatibility to be present as the object is associated with a left-right movement (as opposed to upwards/downwards movement of the finger) without having previously observed the hand stimulus. In line with our predictions no imitative compatibility effects were present for the object. However, as discussed in **Section 3.1.4.2** no significant effects of orthogonal spatial compatibility were present either. Importantly, in both experiments 3 and 4, imitative compatibility was not present only in the blocked finger first group, but not in the object first group, which suggests that this effect is due to seeing the hand stimulus first. This supports the explanation that when participants see the finger first, they carry over this prior knowledge of the human movement to ‘believe’ that the object movement represented, or was somehow associated with the hand movement they had previously observed. This suggests that seeing the finger influenced how they viewed the object, leading to participants to think of the object movement as if it were like the finger movement and respond to it as such. This finding supports studies which have found that beliefs and prior knowledge/information about a given stimulus can modulate the strength of imitative compatibility effects produced for that stimulus (Stanley et al., 2007; Liepelt and Brass, 2010), as discussed in **Section 1.7.1**. The fact we have replicated the same effect in a different group of participants supports a new ‘implicit belief’ explanation for the observation that imitative compatibility effects for the non-biological stimulus tend to be significant in studies presenting biological and non-biological stimuli in separate blocks.

3.1.5 Conclusion

In experiment 4, we found automatic imitation effects were present when using a rotated version of our automatic imitation paradigm, despite orthogonal spatial compatibility being pitted against automatic imitation. In the mixed group, we observed significant imitative compatibility effects for the finger, but no significant orthogonal compatibility or automatic imitation effects were produced for the object. Replicating the effect observed in experiment 3, in the blocked group ‘finger first’ group, automatic imitation was observed not only for the finger, but also for the object stimulus; suggesting that viewing the hand first influenced their perception of the object stimulus such that they believed the object movement was somehow associated with or reflected a human generated movement, causing imitative compatibility to be present for the object. In this respect, participants seem to have created their own ‘belief’ regarding the similarity or association between the finger and object movements. These findings suggest a possible alternative explanation to Gowen and Poliakoff (2012) attentional hypothesis to explain the trend of imitative compatibility for non-biological stimuli when biological and non-biological stimuli are presented in separate blocks of trials. The implication of this finding is that subtle top-down beliefs or prior experience can have a significant influence on imitative compatibility effects, and that further investigation of possible carry-over effects of prior observation of human movement should be undertaken in experiments presenting biological and non-biological stimuli in separate blocks.

3.2 Experiment 5 - Introduction

The results of experiments 3 and 4 have indicated that automatic imitation effects can be modulated by prior knowledge or self-created beliefs. Similarly, as discussed in detail in **section 1.7.1** a number of studies have demonstrated that explicitly manipulating participant’s belief’s regarding the agency of a stimulus modulates the strength of the imitative compatibility effects produced. Importantly, this occurs in situations in which the stimulus presented remained constant, and only the instruction regarding the agency of the stimulus was changed (Stanley et al., 2007; Liepelt and Brass, 2010; Longo and Bertenthal, 2009) thus avoiding possible low level stimulus saliency confounds (Jansson et al., 2007). However, an open question remains as to exactly how beliefs regarding agency modulate imitative compatibility effects. There are two equally plausible explanations for these findings: 1) an attentional hypothesis whereby belief regarding stimulus agency could directly modulate the amount of attention participants direct to the stimulus or, 2) a true belief effect, in which imitative compatibility is directly modulated by the knowledge that the stimulus movement is human/intentional or non-human, whereby the MNS may be up-regulated or inhibited according to one's belief regarding stimulus agency.

In experiment 4 we found no evidence for orthogonal spatial compatibility effects, and additionally the automatic imitation effects obtained were weaker than in previous experiments. We therefore in experiment 5 we aimed to increase the size of the automatic imitation effects, and potentially increase the size of orthogonal spatial compatibility effects. Three main changes have been made, when compared with experiment 1-4. Firstly, stimuli were presented on a larger computer screen (as opposed to a smaller laptop). Secondly, the size of both the stimuli was increased; 3) the size and luminance of the object stimulus itself was increased to more closely match the size of the hand presented, in order to minimize stimulus saliency confounds **(Appendix C1, C2 and C3).** The larger square was made to match the size of the fist of the hand, and the smaller moving square was made into a larger moving rectangle in order to match the size of the entire index finger (as opposed to the finger nail).

Using the rotated paradigm, we aimed to further investigate the effect of belief regarding agency on imitative compatibility effects in experiment 5. We presented the stimuli in the same specific order for each participant: 1) object, 2) finger, 3) object, 4) object (belief condition). In the first section of the experiment, when participants were initially shown the object stimulus only, we expected to establish the baseline level of orthogonal spatial compatibility for the object. Because the participants have not seen the hand stimulus, we would not expect to see imitative compatibility effects for the object stimulus initially. In the second section of the experiment, we expected to establish a baseline level of automatic imitation for the hand stimulus. In the third section of the experiment, if participants noticed the similarity between the finger and object movement, we expected to see a carryover effect, whereby participants would show imitative compatibility for the object due to associating the movement with the previously observed hand movement (as in the blocked 'finger first' group in experiment 3 and 4). In between the third and fourth sections of the experiment belief was manipulated. In the fourth and final section of the experiment we aimed to compare the imitative compatibility effect produced with that of section 1 of the experiment.

Our primary aim was to investigate whether we could replicate previous studies which have found that manipulating participant's beliefs regarding the agency of the stimulus modulates imitative compatibility effects. We hypothesized that if belief modulates imitative compatibility effects, then we would expect that the imitative compatibility effects induced by the observation of the object movement would be enhanced when participants believed that the object movement was generated using a human movement, relative to when no instruction was given regarding stimulus origin. If an effect of belief is present an interaction between condition and compatibility should be present.

Furthermore, we were interested in determining whether the effect of belief regarding agency is due to increased attention or are due to a true effect based on beliefs about stimulus agency. In the experiment, we manipulated participant's beliefs regarding the agency object stimulus movement, by informing them that the object movement was generated from a human finger movement. Importantly, the current rotated version of the experiment allows us to dissociate automatic imitation from spatial compatibility and orthogonal spatial compatibility effects, potentially allowing us to distinguish between the two possible interpretations of the effect of belief regarding stimulus agency. If the effect represents a true 'belief' effect, we would expect to see increased automatic imitation indicated by a positive compatibility effect for the object stimulus in the manipulated belief condition. Alternatively, if the effect of belief does not represent a true belief effect, and is produced due to increased attention to the object stimulus following the belief manipulation, we would expect to see increased orthogonal spatial compatibility (a negative compatibility effect).

3.2.1 Methods

3.2.1.1 Participants

24 right-handed healthy individuals (20 female); however, one participant's data was excluded from analysis due to not complying with the instructions (responding incorrectly by pressing instead of releasing in one of the blocks). The mean (±SD) age of the remaining 23 participants was 25.09 (± 3.03) years, and the mean (±SD) laterality quotient was 83.12 (±19.14). The study consisted of a single testing session lasting approximately 90 minutes, and participants were paid £8 for their participation.

3.2.1.2 Apparatus and materials

As in experiment 4, participants observed a series of images, of a human hand rotated 90 degrees counter-clockwise executing upwards or downwards movements of the right index finger. However, the following changes were made to the experimental set-up. Stimuli were presented on larger a 40.5cm x 30.5cm computer monitor (as opposed to the smaller laptop screen as used in previous experiment). In addition, participants were seated slightly further away from the computer screen in this experiment (80cm). The visual angle of the stimulus image was approximately 8.2° x 10.2°. This alteration was made to facilitate the eye movement recordings that were incorporated in experiment 7. In addition the size, dimensions, colour and brightness of the object stimulus were altered to more equally match and therefore more closely resemble the hand stimulus **(Figure 44 and Appendix C2 and C3)** and consisted of a large stationary square and a smaller rectangle which moved in either a rightwards or leftwards direction.

3.2.1.3 Design and procedure

The same sideways automatic imitation paradigm was used as in experiment 4 **(Figure 43)**. The experiment consisted of a total of 768 trials. Practise trials were included as described in experiment 4 **(section 3.1.2.3)**. The four parts of the experiment were split into sets of 192 trials, as described in experiment 4. The order of presentation of the four parts remained constant throughout the experiment. Within each set of 192 trials the same breaks (every 48 trials) were given, and the same counterbalancing of response type was implemented, as described in experiment 4.

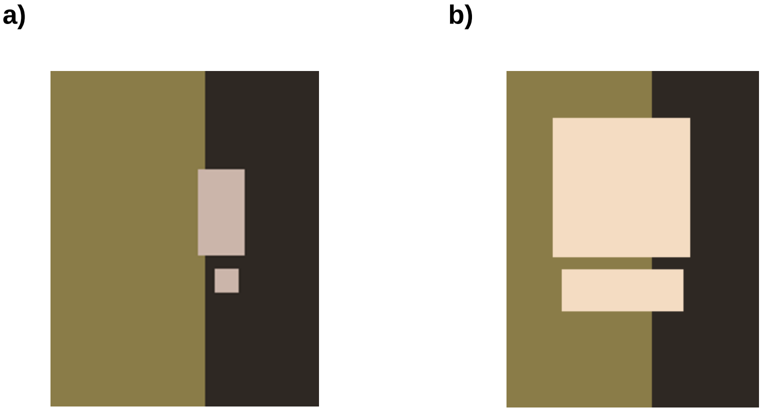


Figure 43: Single frame of a) old version of object stimulus used in experiments 1-4 b) new larger and brighter version of object stimulus used in the current experiment

Prior to Section 4 (belief condition) of the experiment, participants were informed that the object stimulus was generated from the human finger they had observed earlier in the experiment; the smaller moving block representing the movement of the index finger and the larger stationary block representing rest of the hand. Participants were told that the moving block tracked the movement of the finger exactly, and therefore was a block representation of the human finger movement.

Consistent with previous experiments participants were required to complete the ELI questionnaire for handedness **(Appendix A1)** and the EQ empathy questionnaire **(Appendix A2)**. In addition, after section 3 and section 4 (belief condition), participants completed two additional belief questionnaires **(Appendix A5)**. The first questionnaire aimed to measure whether there was any difference between how the object was perceived before and after seeing the hand stimulus. We hypothesized that the object may be perceived to be more hand-like after seeing the hand. This questionnaire was completed after seeing the object for the second time (prior to section 4: belief), however some of the questions were to be completed in relation to the first time they had seen the object compared to the hand, and the some of the questions were to be completed regarding the second time they had seen the object compared to the hand stimulus. The second questionnaire was which included some additional questions regarding the belief manipulation completed at the end of the experiment following Part 4 (belief) participants completed a final questionnaire about the stimuli. The questionnaire aimed to measure the extent to which participants had been affected by the belief manipulation.

3.2.2 Results

3.2.2.1 Analysis of error data

The same exclusion criterion used in previous experiments was applied. This resulted in a total loss of 1.14% of trials on average. In addition the same error types **(section 2.1.3.1)** could be incurred in this experiment.

Overall, participants in both the mixed and blocked group made a low level of errors **(Table 14 and Table 15)**; therefore no individual participant's data was removed from the study. The error participants were most prone to was the no-go error.

Table 14: Mean % Anticipation errors, no-go errors and second response errors calculated as a percentage of the total number of trials where the error could occur for each type of error overall across the experiment. **Bold type** represents compatible trials.

Type of Error (total number of trials where error could occur)	Mean % Errors (± SE)
Anticipation error (672)	0.21 (± 0.03)
No-go error (96)	2.46 (± 0.00)
Second response error (672)	0.00 (± 0.00)

Table 15: Mean no-go and anticipation errors (± SE) for each stimulus. No-go errors were made out of a potential 96 and anticipation errors were made out of a potential 672. **Bold** type represents compatible trials.

Stimulus	Mean No-go errors (± SE)	Mean Anticipation errors (± SE)
Section 1: Object	**0.72 (± 0.17)** 1.04 (± 0.25)	**0.00 (±0.02)** 0.01 (± 0.03)
Section 2: Belief	**0.77 (± 0.36)** 1.18 (± 0.26)	**0.01 (±0.02)** 0.01(± 0.03)
Section 3: Finger	**1.09 (± 0.27)** 1.04 (± 0.23)	**0.03 (±0.05)** 0.02 (± 0.04)
Section 4: Object	**0.86 (± 0.32)** 1.49 (± 0.29)	**0.03 (± 0.04)** 0.02 (± 0.04)

3.2.2.2 Analysis of reaction time data

Overall mean RTs (ms) (± SE) are presented in **Table 16**. Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects.

Table 16: Mean RTs (ms) (±SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (*p* < .05).

Stimulus	SOA	Mean RT (ms) (± SE)
Object (Section 1)	0	**345.20 (± 11.01)** 345.14 (± 12.20)
	120	**315.10 (± 8.40)** 322.20 (± 9.05)*
	280	**299.37 (± 9.12)** 295.02 (± 8.02)
Finger (Section 2)	0	**349.59 (± 11.69)** 350.24 (± 12.55)
	120	**311.61 (± 8.03)** 320.60 (± 10.19)
	280	**302.92 (± 8.77)** 305.66 (± 8.46)
Object (section 3)	0	**336.39 (± 9.89)** 331.35 (± 9.58)
	120	**311.42 (± 8.25)** 313.69 (± 8.36)
	280	**391.45 (± 8.01)** 286.79 (± 7.46)
Belief (section 4)	0	**343.99 (± 11.12)** 340.56 (± 12.21)
	120	**308.62 (± 8.11)** 305.70 (± 8.95)
	280	**287.32 (± 9.27)** 287.67 (± 9.04)

An initial mixed design (2 x 4 x 2 x 3) repeated measures ANOVA was conducted on participants' mean RTs; with response type (press/release) x condition (object1/hand/object2/object3) x compatibility (compatible/incompatible) x SOA (0, 120, 280) as within-subjects factors. No significant main effects of response type or interactions with response type were present. Therefore, mean RTs across press and release response types were averaged and a 4 x 2 x 3 repeated measures ANOVA was conducted on this averaged data.

This ANOVA revealed that there was no significant interaction between condition and compatibility (F(3,66) = 1.420, p = .245). Significant main effects and interactions not directly relevant to the hypotheses are presented in **Appendix B3**.

Paired t-tests between compatible and incompatible RTs indicated a significant compatibility effect for the object **(Figure 44)** at 120ms; however, no significant interactions with compatibility were present.

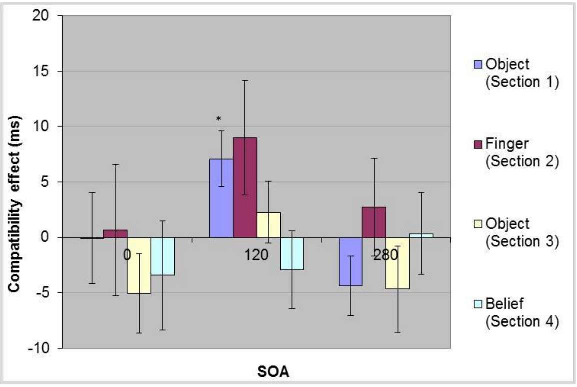


Figure 44: Figure shows the compatibility effects for each of the 4 parts of the experiment, for each SOA.

3.2.2.3 Analysis of questionnaire data

Mean questionnaire scores for each group and overall are displayed in **Table 17.**

Table 17: Mean Questionnaire scores. In response to statement 1-6: a score of 10 represents 'agree'; 5 represents 'neither agree nor disagree' and 0 represents disagree. In response to questions 7-10: a score of 10 represents 'very much'; a score of 5 represents 'to some extent' and a score of 0 represents 'not at all'.

Question No	**Question/Statement**	**Mean score**		
		First time object observed (completed after Section 3)	**Second time object observed (completed after Section 3)**	**Belief (completed after Section 4)**
1	Watching the finger grabbed my attention more than watching the block	6.8	6.2	6.1
2	Watching the block grabbed my attention more than watching the finger	3.3	3.5	3.8
3	The clips of the block and the finger were similar in terms of movement	4.5	4.8	7.7
4	The clips of the block and the finger were similar in terms of appearance	2.7	2.8	6.4
5	Seeing the block move made me want to move my own finger	2.0	3.2	4.3
6	Seeing the finger move made me want to move my own finger	5.3	3.8	5.5
7	When you saw the block again, did you think of the object as more of a 'block representation of the hand, compared to when you had seen the block for the first time?	-	3.4	7.5
8	When you saw the block again, to what extent did you think that seeing the hand influenced your perception of the block movement, making the block seem to move in a more hand-like way, compared to when you saw the object the first time?	-	3.4	7.3
9	When you found out that the block movement had been generated by a hand movement how much did you think about this whilst viewing the block for the third time?	-	-	7.4

In contrast with the RT findings, some of the self-reported measures of belief suggest that participants felt that the belief manipulation altered their perception of the object. This is not the case for Question 1 and 3, which indicates participants felt the finger (M = 6.1-6.8) grabbed their attention more than the object (M = 3.3-3.7), and their scores for these questions did not change significantly throughout the experiment. Similarly, although the highest score indicates a neutral score, participant did increase their initial score (M = 1.9) for the statement 'seeing the block made me want to move my own finger' (M = 3.8) the second time they saw the object (after seeing the hand), and then increased their score again after the belief (M = 4.3) which suggests a change in belief about the object, however this increase was not reflected in the RT scores. However, there appears to be a difference before and after the belief manipulation for the questions 3 and 4. For example participants' mean score changed from a neutral (M = 4.5-4.8) to a higher mean score of 7.7 regarding the similarity of the movement, and from 2.6-2.8 to 6.4 for the similarity of appearance of the two stimuli. Similarly, for questions 7 and 9 participant's scores increased from 3.1/3.4 to 7.5/7.3 respectively. Participants also rated question 10 (regarding how much they thought about the block movement being generated from a human hand movement) highly (M = 7.4). In order to test whether there was a statistical difference between questionnaire scores before and after belief, scores for questions 2-5 the first time the object was observed **(Table 17)** were collapsed to create a 'pre belief' score for each participant. Similarly all scores for the questions 2-5 after the belief condition were collapsed to create a 'post belief' score for each participant. A paired t-test was carried out between participants pre/post belief collapsed score which revealed that participants post belief scores were significantly higher than in the pre-belief condition ($t(22) = -6.779$, $p = .000$). In addition, a pre-belief score for the second time the object was observed, and a post belief score for the after belief condition was generated based by collapsing scores for questions 7 and 8 in each condition. Scores were significantly higher pre-belief compared to post belief ($t(22) = -5.333$, $p = .000$).

3.2.2.3.1 Relationship between self-reported belief questionnaire and EQ scores

A correlation test was carried out between participant's self-reported questionnaire scores for questions 7, 8, 9 (using scores for post belief condition) and mean empathy scores. We chose these specific questions to correlate because they measure the extent to which the participant reported to believe the information given in the belief manipulation, which we hypothesized may be more 'empathy related'. We predicted that people with a higher mean empathy score might also rate these questions highly, as they might be more inclined to believe the belief manipulation than those with lower empathy scores. A significant positive correlation was found between statement 7 and participants' empathy questionnaire scores ($r(23) = .447$, $p = .032$) **(Figure 45)**. This indicates those participants who were more empathetic tended to report to have thought of the object as a block representation of the hand; however less empathetic individuals reported they did not think of the object as hand-like even though they had been instructed that it was the case. There was no correlation between empathy and questions 8 ($r(23) = .324$, $p = .132$) or 9 ($r(23) =$

.316, *p* = .142). There were no significant correlations between AQ scores and questions 7, 8 or 9 (*p* >.144).

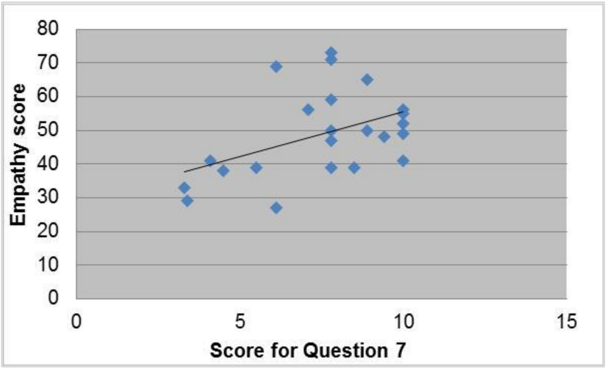


Figure 45: Positive correlation between question 7: ‘when you found out that the block movement had been generated by a hand movement did you think of the block as more of a ‘block representation’ of the hand compared to when you had seen the block for the first time?’ and empathy scores

3.2.2.3. Exploring the initial compatibility for the object stimulus

As there were no significant compatibility effects present we did not correlate all scores and mean compatibility effects. However, as there was an unusual trend in this experiment, whereby participants were initially responding to the object as if it were a hand, we were interested to see whether initial compatibility effects for the object at 120ms were correlated with empathy, AQ or question 5 (‘Seeing the block made me want to move my own finger’).

Therefore, Pearson’s correlation tests were carried out between compatibility effects for the object at 120ms and empathy, AQ and question 5 scores. There was no correlation between initial compatibility effects for the object at 120ms and AQ scores (*r*(23) = .125, *p* = .570). However the negative correlation between initial compatibility effects for the object at 120ms and EQ scores was approaching significance (*r*(23) = -.407, *p* = .054) **(Figure 46)**.

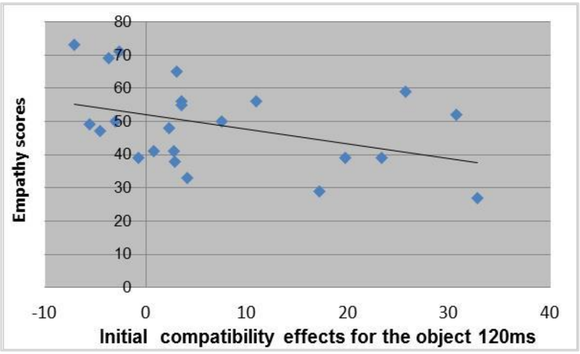


Figure 46: Negative correlation between EQ scores and initial compatibility effects for the object stimulus at 120ms

In line with this, there was a significant negative correlation between EQ scores and scores for question 5 (*r*(23) = -.513, *p* = .012). This suggests that participants with lower EQ scores felt that watching the block made them want to move their own finger, whereas those with higher EQ scores participants did not **(Figure 47)**.

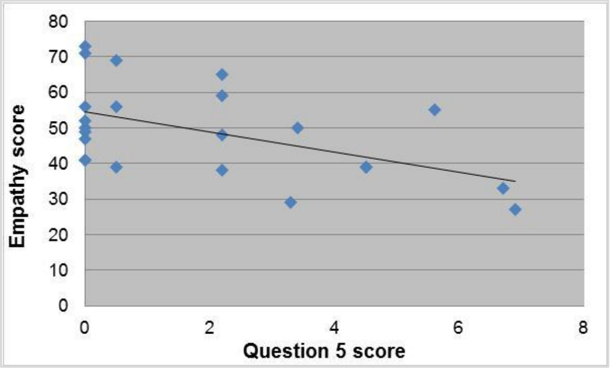


Figure 47: Negative correlation between statement 5: ‘seeing the block move made me want to move my own finger’ and EQ scores

In addition, the positive correlation between question 5 scores and initial imitation of the object stimulus at 120ms was approaching significance (*r*(23) = .362, *p* = .090).

3.2.3 Discussion

Experiment 5 has produced three main findings. Firstly, it is important to note the absence of the typical significant automatic imitation effects for the finger stimulus in this experiment (although the ‘trend’ of compatibility effect for the finger at 120ms SOA was present). Secondly, there was unexpectedly an initial significant imitative compatibility for the object stimulus at 120ms in the first part of the experiment. Thirdly, the belief manipulation was unsuccessful, as there were no imitative compatibility effects for the object stimulus following instilling the belief that the object stimulus was generated from a human finger movement. On the contrary, the belief manipulation appeared to have the opposite effect to that expected; with the initial imitation occurring for the object at 120ms at the start of experiment significantly decreasing the second time they saw the object and no imitation at all for the object following the belief manipulation. As there no significant imitative compatibility effects were present, we did not correlate questionnaire findings with imitation**,** however; correlations were found between empathy, imitative compatibility effects and questionnaire results which may provide some insight as to why imitation was initially produced for the object stimulus. These results will now be discussed in further detail below.

3.2.3.1 Loss of imitation

Although we increased the size of the stimuli presented, in order to strengthen automatic imitation effects, automatic imitation effects were completely absent in the current experiment. The lack of automatic imitation for the finger stimulus is an unusual finding, as we have replicated findings of stronger automatic imitation for the finger compared to the object in all of the previous experiments documented in this thesis, with significant compatibility effects being present for the finger stimulus. It is possible that the loss of imitation in this experiment is due to the set order of the experimental blocks, with the hand stimulus (section 2) always following the object stimulus (section 1). It is possible that attention to the finger stimulus in this experiment was reduced because the hand stimulus was always seen after the object stimulus. This is in line with the finding of larger imitative compatibility effects for the finger in the finger first group compared to the object first group in experiment 4.

However, one of the main changes made in this experiment in comparison to our earlier experiments is the change in size and shape of the object stimulus to more closely match the hand stimulus (to reduce stimulus saliency confounds), and the increase in size of both the hand and object stimuli presented on the larger computer screen (as opposed to laptop). Although our objective in increasing the size of the object stimuli was to reduce stimulus saliency confounds, and increasing the size of both stimuli in order to increase automatic imitation effects, it is possible that this may have actually increased the spatial spread of attention for both types of stimuli leading to more variable results and large errors bars, causing the lack of significant compatibility effects for the finger observed in this experiment.

3.2.3.2 Initial imitation of the object stimulus

The most unusual finding in this experiment was that there was a significant initial imitative compatibility effect for the object stimulus in part 1 of the experiment. As there was no apparent reason for participants, who were naïve to the experiment and had not seen the hand stimulus before, to associate the rotated object with a finger movement, this was a particularly interesting and unexpected finding. This goes against the original hypothesis that an orthogonal spatial compatibility effect should be present for the object, and no imitative compatibility should be present initially for the object.

There are two possible explanations for this finding. Firstly, the trend for automatic imitation to be present for the object stimulus may be due to individual differences in participants’ initial conscious or unconscious beliefs about the origin of the object stimulus. Secondly, this finding may suggest that participants were spontaneously anthropomorphizing the object stimulus, and actually saw the movement of the object as being human. This effect may have emerged in this particular experiment due to the changes in the shape of the object stimulus, which was altered to create a more oblong, finger-like shape in order to more closely match the hand stimulus, therefore making the object appear more hand/finger like. One of the predicted sources of influence of anthropomorphism includes perceived similarity of morphology and motion the non-human agent (Epley et al., 2007). This supports the idea that the change in shape/morphology, making the object more closely resemble a human finger, in combination with biological movement kinematics, could have contributed to the initial anthropomorphism of the object. In addition we are more likely to anthropomorphise ambiguous stimuli (Epley et al., 2007), such as that used in the current experiment.

In addition, some of the questionnaire correlations support the theory that some participants, particularly those with lower empathy scores, may have been inclined to initially anthropomorphise the object stimulus. For example, the positive correlation between initial compatibility effects for the object at 120ms and scores for question 5 ‘seeing the block move made me want to move my own finger’ with regard to the first time they saw the object stimulus was approaching significance (*p* = .090). This could been interpreted as supporting the idea that participants were anthropomorphising the object stimulus, as we would have expected participants to give this statement a low score if they saw the object purely as a rectangle moving from left to right. Therefore it is possible that participants were anthropomorphising the object stimulus, therefore causing imitative compatibility effects to be generated. Furthermore, the negative correlation between initial compatibility effects for the object at 120ms and empathy scores was approaching significance (*p* = .054). This suggests that less empathetic participants were more likely to initially show compatibility effects for the object. Although one might initially be inclined to predict people with higher empathy scores would be more likely to anthropomorphize an inanimate object, research into the psychological determinants of anthropomorphism provides a possible plausible explanation as to why the low empathy group might anthropomorphise more than the high empathy group. According to the SEEK three factor theory of anthropomorphism, one of the key psychological determinants of anthropomorphism is sociality – the need or desire to connect with other people (Epley et al., 2007). Anthropomorphized agents can act as powerful agents of social connection when human connection is lacking. Experimental evidence suggests that even momentary feelings of social rejection or isolation, induced by watching a movie clip intended to induce feelings of loneliness, can increase the tendency to anthropomorphise one’s pet in a manner that may effectively alleviate social disconnection and can also increase the extent to which people report believing in anthropomorphized supernatural agents (Epley et al., 2007). The SEEK theory therefore suggests that chronic loneliness and social disconnection may certainly increase the likelihood of anthropomorphism taking place, satisfying the human need for social connection by creating a humanlike connection with non-human agents. Therefore this theory predicts that anthropomorphism increases when people feel a lack of social connection to other humans and decreases when people feel a strong sense of human connection. It is therefore plausible, that someone who has low empathy, and more difficulty understanding the feelings of others, might feel socially disconnected with other people because of this. If this was the case, it could provide a possible explanation as to why participants with low empathy scores might actually anthropomorphise the object stimulus initially, as opposed to those in the high empathy category, who may already feel a strong sense of human connection. Interestingly in line with this, there was a significant negative correlation (*r*(23) = -0.513, *p* = .012) between empathy scores and scores for the statement ‘seeing the block move made me want to move my own finger’. This suggest that less empathetic participants (who may have anthropomorphised the object) felt that watching the block made them want to move their own finger, whereas more empathetic participants (who showed less imitation of the object) did not. Therefore, the less empathetic participants may on some level have actually been aware they were anthropomorphizing the object; or their attention may be more strongly drawn to the object making anthropomorphism more likely to occur.

3.2.4.3 Failure of belief manipulation

We predicted that if prior knowledge regarding agency modulated imitative compatibility behaviour we would see enhanced imitative compatibility following the belief manipulation. However the data suggests participants initially saw the object as hand-like in section 1 of the experiment, and this belief decreased following seeing the hand and decreased further in sections 3 and 4 when the object was presented again. The fact that the effect went in the opposite direction could reflect a decrease in attention to the stimulus as the experiment progressed. It is unclear whether the decline in automatic imitation is due to reduced attention or increased inhibition of imitation. As mentioned previously, it has been demonstrated that the compatibility effects from an automatic tendency to imitate declined significantly across a block of trials (whereas the effects of spatial compatibility remained constant or increased slightly) (Catmur and Heyes, 2011). It is therefore possible that automatic imitation effects may have naturally decreased throughout the 90-minute experiment due to a lack of motivation, or a reduction in interest in/attention to the object stimulus as the experiment progressed.

Alternatively, it is possible that although participants initially thought of the object as hand-like as shown by the initial anthropomorphism of the object in this particular experiment, conversely, observation of a real biological hand stimulus in section 2 made the object appear comparatively less biological, leading to the subsequent reduction in the initial imitation for the object in section 3 and 4 of the experiment. One finding which supports the idea the belief was not successfully instilled, is that RTs are faster in the belief condition compared to RTs for the object in section 1. Although this makes sense in the sense that participants may have reacted faster due to being well practised towards the end of the experiment, pre-empting findings in later experiments, we found that where the belief manipulation was successful, significantly slower RTs were present in the belief condition, which we attributed to mental rotation of the stimulus in the belief condition. This therefore supports the idea that participants did not believe the object represented a human finger movement and hence no mental rotation of the stimulus took place. One further possibility is that participants may have changed attentional strategy towards the end of the experiment, and paid more attention to detecting the yellow flash at the periphery of the screen, thus causing a lack of attention to the movement of the stimulus as the experiment went on. This may have led to faster RTs in the belief condition, while imitative compatibility effects were absent.

Some of the questionnaire findings support the latter explanation. On visual inspection the questionnaire findings appear to suggest that the belief manipulation *did* have an effect on how participants viewed the object stimulus; however this reported belief effect was not reflected in the RT time results, and there was no interaction between reported beliefs and compatibility effects. In line with the failure of the belief manipulation, paired t-tests revealed that the difference between questionnaire scores before and after belief, did not quite reach statistical significance ($t(22) = -1.906$, $p < .069$), the overall pre belief score being lower (M = 2.92) than the overall post belief score (M = 3.37), suggesting participants did not feel their beliefs were successfully manipulated. In Press et al. (2006), there was a similar dissociation between self-reported belief scores and automatic imitation effects.

A questionnaire used to assess subject's beliefs about stimulus agency suggested that participants were significantly affected by the belief manipulation, scoring stimuli presented during the 'human' instruction condition as more animate; however the amount of automatic imitation was unaffected by belief instruction**.** The discrepancy between the fact that the difference between pre and post-belief scores was approaching significance (suggesting a trend towards a self-reported effect of belief), but was no modulation of automatic imitation based on belief regarding agency suggests one of two possibilities: 1) the effect of belief on automatic imitation may be more of a subconscious/implicit effect which may not something that participants can correctly introspect about; 2) participants may have answering in accordance with their inferred expectations of the experimenter (based the information given by the experimenter during belief manipulation) as opposed to responding in accordance with their true beliefs regarding the agency of the object stimulus. Therefore, it is possible that participants may not have been convinced by the belief manipulation, but may have inferred that the experimenter's aim or expectation was for them to believe the information they were given (i.e. that the object movement was generated by a human finger movement), and therefore answered in accordance with the inferred experimenter's expectations.

In the current study, a number of measures were in place to reduce possible demand effects throughout the study, for example for the RT data, as participants were naïve to the purpose of the experiment and were never explicitly asked to imitate at any point, but simply to press or release the button in response to the yellow flash. However, although it was stressed that participants should feel free to be completely honest in answering the questionnaire, as all responses would be scored anonymously, and participants were not observed whilst completing the questionnaire; there is the possibility that participant's behaviour was altered due 'demand effects', and scored the questionnaire based on what the inferred expectations of the experimenter.

One argument in favour of participants giving the score based on inferred expectations of the experimenter is that interestingly, there was a significant positive correlation between the statement 'when you found out the block movement had been generated by a hand movement did you think of the block as more of a 'block representation' of the hand compared to when you had seen the hand for the first time' and empathy scores.

This suggests participants who reported to be more empathetic reported to have thought of the object as a block representation of the hand; however individuals who reported to be less empathetic did not think of the object as hand-like even though they had been instructed that it was the case. As the experimenter had previously instructed the participant that the block was in fact a block representation of the hand, this is presumably what the participant expected the experimenter wanted to hear, so could suggest one of two things. Firstly, more empathetic individuals might be more likely to believe what the experimenter tells them, or secondly that more empathetic individuals are more likely to respond based on the inferred expectations of the experimenter.

3.2.5 Conclusion

In experiment 5, we aimed to investigate whether manipulating the top-down factor of belief regarding the agency of the object stimulus by instilling a human belief regarding stimulus agency would lead to stronger imitative compatibility effects for the object relative to when the participant was given no specific information about the origin of the object. However, the belief manipulation had the opposite effect to that expected. Imitation was initially present for the object but completely absent following the belief manipulation. The initial imitative compatibility effect for the object is difficult to explain, but may be due to individual differences in participants' initial beliefs about the origin of the object stimulus. It is possible that initial anthropomorphism of the object occurred in this particular experiment due to the change in shape of the object, which was altered to a more oblong finger-like shape in order to more closely match the hand stimulus. Furthermore, seeing the real human hand stimulus may have led to the subsequent reduction in imitation for the object as it appeared less biological following observation of the real hand.

3.3 Experiment 6 - Introduction

In experiment 6 we aimed to investigate whether or not the initial imitative compatibility for the object observed in experiment 5, would be replicated in another group of participants. As discussed, one possible explanation for the failure of the belief manipulation in experiment 5 is that that inhibition of imitative compatibility effects for the object stimulus may occur after seeing the hand stimulus, due to the fact that the object may appear much less human after seeing a real human hand. Therefore, in particular, we were interested to see if an effect of belief would be present if participants never saw the hand stimulus during the experiment. In experiment 6, participants viewed the object stimulus followed immediately by the belief manipulation, following which the object was observed again. Importantly, the hand stimulus was never presented. We hypothesized that if that seeing the hand stimulus did lead to an inhibition of imitative compatibility effects for the object (consequently making the object appear comparatively less biological), then if participants do not see the hand stimulus at all, an effect of belief may be present. If an effect of belief is present, we would expect to see an interaction between compatibility and condition.

3.3.1 Methods

3.3.1.1 Participants

30 right-handed healthy individuals (21 female), with a mean (±SD) age of 24.78 (± 5.68) years were recruited. The mean (±SD) laterality quotient was 92.13 (±17.20). The study consisted of a single testing session lasting approximately 1 hour, and participants were paid £5 for their participation.

3.3.1.2 Design and procedure

The design and procedure of experiment 6 was similar to that of experiment 5, with the exception of the following change: participants did not see the hand stimulus and the experiment only consisted of two parts. Initially, they were presented with the object stimulus, then in the second part the belief manipulation was then carried out, during which participants were told that the object movement had been generated from a human finger movement, as in experiment 5. The two parts of the experiment were split into sets of 192 trials, as described in experiment 4, giving a total of 384 trials. Within each set of 192 trials the same breaks (every 48 trials) were given, and the same counterbalancing of response type was implemented, as described in experiment 4. Participants completed a questionnaire about the extent to which the belief manipulation altered their view of the object stimulus to make it seem more biological (hand-like), and to what extent the belief manipulation was successful. They recorded their answers on a 10-point Likert scale; with 0 representing ‘not at all’, 10 representing ‘very much’ and 5 representing the neutral response ‘to some extent’. Participants also completed the EQ empathy questionnaire. As we were particularly interested in the belief aspect of the experiment in this study, we only included questions relating to self-reported belief regarding agency of the object, following the belief manipulation. The questionnaire was therefore completed at the end of the experiment, after the belief manipulation and viewing the object for the second time (with belief).

3.3.2 Results

3.3.2.1 Analysis of error data

The same exclusion criterion used, and the same error types could be incurred as in previous experiments. This resulted in a total loss of 1.24% of trials on average.

Overall, participants made a low level of errors **(Table 18 and 19)**; therefore no individual participant's data was removed from the study. There were no second response errors and a very low number of anticipation errors in this experiment. The error participants were most prone to was the no-go error. No second response errors were made.

Table 18: Mean % Anticipation errors, no-go errors and second response errors calculated as a percentage of the total number of trials where the error could occur for each type of error overall across the experiment. **Bold type** represents compatible trials.

Type of Error (total number of trials where error could occur)	**Mean % Errors (± SE)**
Anticipation Error (336)	0.63 (± 0.13)
No-go Error (48)	5.03 (± 0.87)

Table 19: Mean % no-go and anticipation errors (±SE) for each stimulus. No-go errors were made out of a potential 48 and anticipation errors were made out of a potential 336. **Bold** type represents compatible trials.

Condition	**Mean % No-go errors (± SE)**	**Mean % Anticipation errors (± SE)**
Object	**1.46 (± 0.54)** 1.67 (± 0.20)	**0.03 (± 0.03)** 0.03 (± 0.04)
Belief	**3.96 (± 0.45)** 2.99 (± 0.28)	**0.04 (± 0.05)** 0.06 (± 0.05)

3.3.2.2 Analysis of reaction time data

Overall mean RTs (ms) (±SE) are presented in **Table 20**. Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects.

Table 20: Mean RTs (ms) (±SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (*p* < .05).

Stimulus	SOA (ms)	Mean RT (ms) (± SE)
Object	0	**297.47 (± 7.26)** 299.50 (± 8.59)
	120	**285.44 (± 7.28)** 287.16 (± 6.70)
	280	**267.70 (± 7.28)** 270.12 (± 7.21)
Belief	0	**343.02 (± 11.56)** 342.99 (± 11.15)
	120	**293.78 (± 7.90)** 300.14 (± 9.40)
	280	**279.39 (± 7.72)** 281.72 (± 8.12)

An initial repeated-measures ANOVA with response, condition (belief/no belief), SOA and compatibility as within-subjects factors was conducted on mean RTs. There was no main effect of response or interactions with response therefore RTs were averaged across press and releasing responses.

An ANOVA averaged across pressing and releasing responses, with condition, SOA and compatibility as within-subjects factors was conducted. This ANOVA revealed that there was no significant interaction between condition and compatibility (F(1,29) = .105, p = .748) **(Figure 48)**. Significant main effects and interactions not directly relevant to the experimental hypotheses are presented in **Appendix B4**.

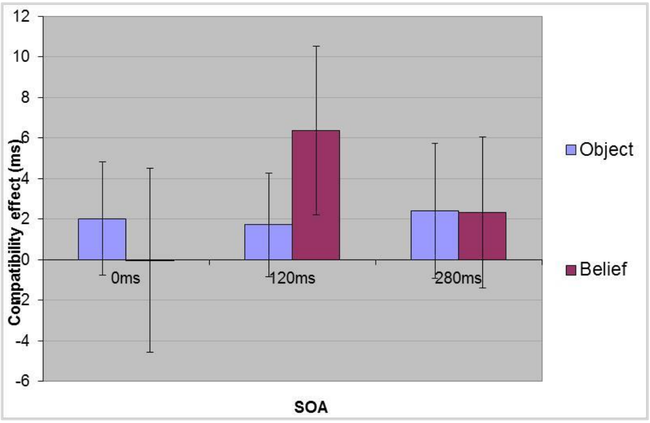
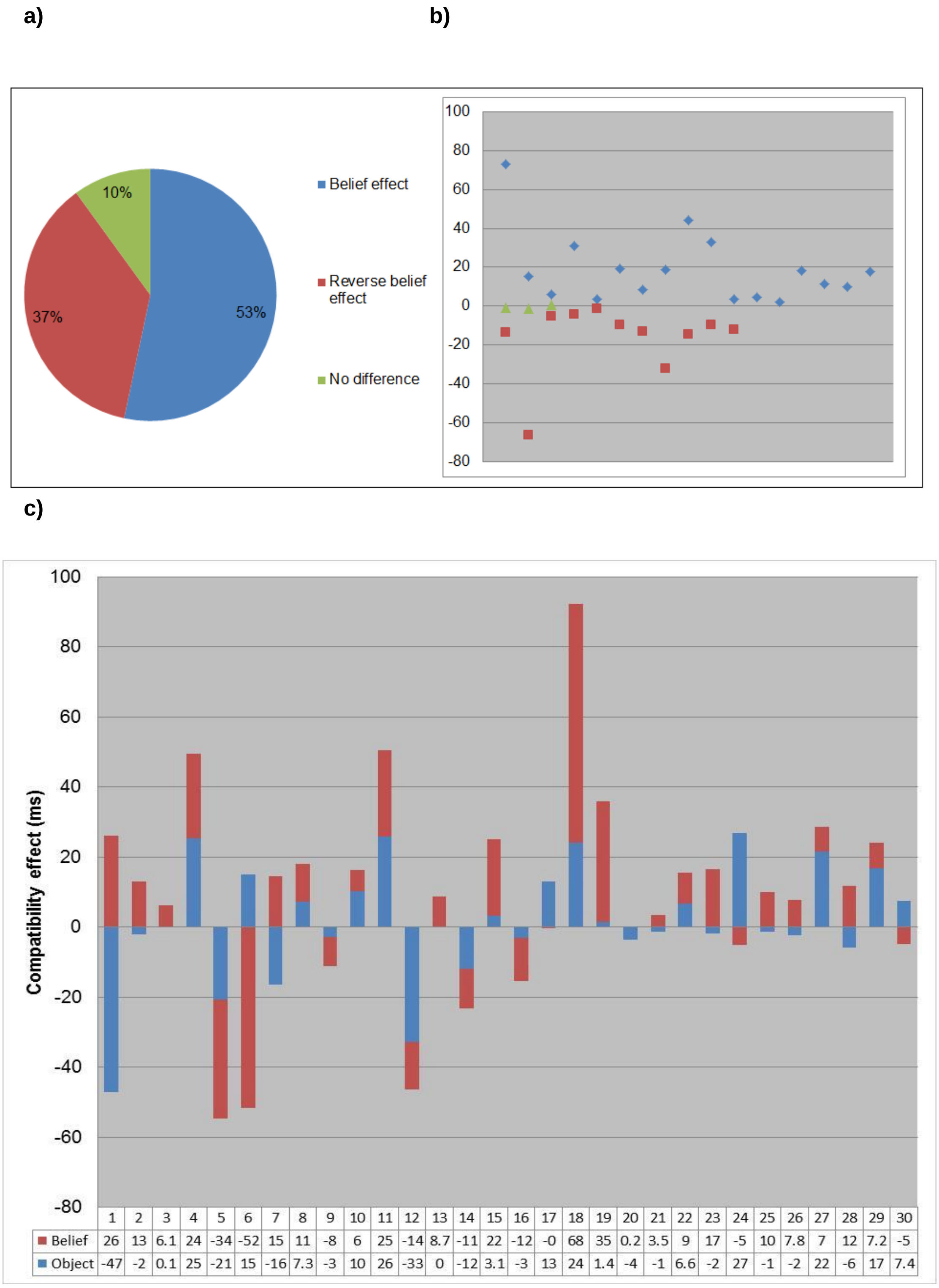


Figure 48: Figure shows mean compatibility effect (ms) for the object without the belief manipulation and after the belief manipulation at all three SOAs

3.3.2.4 Exploring a potential belief effect

Although a trend was present suggesting that the belief manipulation had an effect in the experiment **(Figure 48),** this was not a significant effect due to large error bars. Further investigation of the emerging patterns of compatibility effects in this experiment, confirms the wide variability in patterns of responding among participants. Although initial compatibility effects for the object are low in this experiment, 13 participants actually started with a positive compatibility effect above 3 for the object initially (before belief) at 120ms SOA. 17 participants started with a negative compatibility or compatibility effect below 3ms.

Overall, 14 participants appeared to be affected by the belief manipulation i.e. their initial compatibility effect increased after the belief manipulation. Of these 14 participants, 11 followed the originally hypothesized trend, going from a negative or low compatibility effect (below 3) for the object initially to a higher positive compatibility score (above 3). The remaining 3 participants went from a positive initial compatibility effect for the object (above 3) to an even higher positive compatibility effect after belief. However, 7 participants went in the opposite direction, indicating the belief manipulation had the opposite effect on these participants, and decreased any initial imitation effects. Of these 7 participants, 5 participants went from a positive compatibility effect initially to a negative compatibility effect (below zero) after belief, and 2 participants went from a positive compatibility effect to a less positive compatibility effect (above 3). In addition, 4 participants had a stable compatibility effect with no significant increase or decrease in compatibility effects (3ms difference or less) following the belief manipulation, and 5 participants had a negative compatibility effect for both conditions indicating they had no compatibility effects before or after belief (3 of these went from more negative to less negative after belief, and 2 went from less negative to more negative after belief).



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
🟥 Belief	26	13	6.1	24	-34	-52	15	11	-8	6	25	-14	8.7	-11	22	-12	-0	68	35	0.2	3.5	9	17	-5	10	7.8	7	12	7.2	-5
🟦 Object	-47	-2	0.1	25	-21	15	-16	7.3	-3	10	26	-33	0	-12	3.1	-3	13	24	1.4	-4	-1	6.6	-2	27	-1	-2	22	-6	17	7.4

Figure 49: a) Pie chart showing percentage of participants who showed a belief effect (a difference greater than 2); a reverse belief effect (a difference less than -2) or no change in belief (a difference between -2 and 2); **b)** Scatterplot of participants belief effects; **c)** Figure demonstrating the variability in compatibility effects in this experiment. Numbers 1-30 represent each participant. The blue bars show the participants initial compatibility for the object and the red bars show participants compatibility effect in the belief condition.

3.3.2.4 Analysis of questionnaire data

Participants completed a questionnaire as a self-reported measure of the extent to which the belief manipulation altered their view of the object stimulus to make it seem more biological, and to what extent the belief manipulation was successful.

Mean questionnaire scores for each group and overall are displayed in **Table 21**.

Table 21: Mean Questionnaire scores. A score of 10 represents 'very much'; a score of 5 represents 'to some extent' and a score of 0 represents 'not at all'.

Q. No	Question	Score
1	When you saw the block for the second time, did you think of the object as more of a 'block representation' of the hand, compared to when you had seen the block for the first time?	**6.87**
2	When you saw the block for the second time, to what extent did you think of the block as a hand compared to when you had seen the block for the first time?	**7.04**
3	When you saw the block for the second time, to what extent do you think that knowing that it represented a hand influenced your perception of the block movement, making the block seem to move in a more hand-like way, compared to when you saw the object the first time?	**6.66**
4	When you were told the block represented a hand movement, how much did you believe that this was true?	**7.88**
5	When you were told the block represented a hand movement, how much did you think about this during the second half of the experiment?	**7.87**

Answers to questions 1-3 on the questionnaire indicate participants did think of the object as representing a hand movement/being hand-like compared to the first time they saw the object; participants scored all three questions between 6.66-7.04 (meaning participants felt somewhere between 'to some extent' and 'very much'). Answers to questions 4 and 5 indicate that participants reported that they were affected by the belief manipulation, as the mean score for the question 'When you were told the block represented a hand movement, how much did you *believe* that this was true?' was 7.91, and the mean score for how much they thought about this during the experiment was 7.66.

3.3.2.4.1 Relationship between belief questionnaire and EQ

Pearson's correlations tests were carried out between the empathy questionnaire scores and an average score for self-reported effects of the belief manipulation (average score collapsed across all belief questionnaire question scores), and mean compatibility effects for each participant at 120ms SOA in both conditions (belief/no belief). This time point was used as the largest compatibility effects were present at the 120ms SOA (although these did not reach significance) in the current experiment, and the largest non-significant compatibility effects were also present at 120ms SOA in experiment 5. The reasoning behind performing these correlations was that although the automatic imitation effects for the object following belief did not reach significance due to the variability between participants, there was a trend towards the belief manipulation being successful. Therefore, we wanted to investigate whether there were any correlations between imitative compatibility effects and empathy that might explain the inter-participant variability in terms of the belief effect.

There was a significant positive between EQ scores and mean belief questionnaire scores (*r*(30) = .370, *p* = .044) **(Figure 50)**.

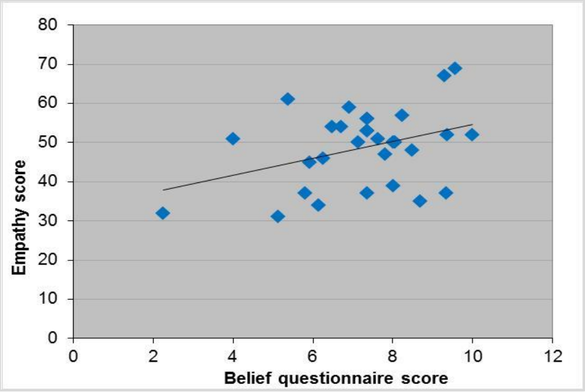


Figure 50: Positive correlation between empathy scores and belief questionnaire average score

There was a significant positive correlation between participant's mean compatibility effects for the object prior to the belief manipulation at 120ms SOA and EQ scores (*r*(30) = .431, *p* = .018 **(Figure 51)**.

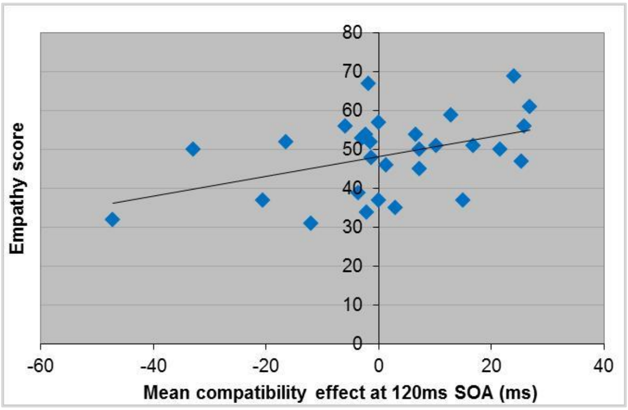


Figure 51: Positive correlation between compatibility effects for the object (before belief) at 120ms SOA and EQ scores

The positive correlation between compatibility effects for the object after the belief manipulation at 120ms SOA and empathy scores also approached significance (*r*(30)=0.344; *p* = .063) **(Figure 52)**.

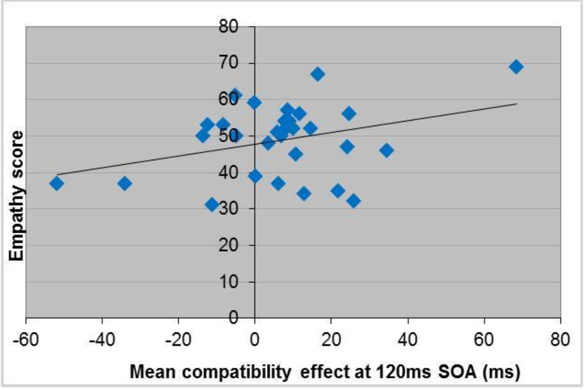


Figure 52: Positive correlation between compatibility effects for the object (after belief) at 120ms SOA and EQ scores

3.3.3 Discussion

3.3.3.1 Absence of initial imitative compatibility for the object stimulus

In experiment 5, initial imitative compatibility effects were present for the object stimulus in section 1 of the experiment prior to the belief manipulation, which we attributed to possible anthropomorphism. It is difficult to explain why initial automatic imitation for the object occurred in experiment 5 but not in experiment 6 as these initial object conditions were identical. It is possible that is that because the two experiments included two completely different participant groups, group differences in initial implicit beliefs regarding the agency of the object stimulus could explain this difference. We explored the possibility that empathy could explain the differences seen between the two experiments. In experiment 5, the analysis suggested that those with lower empathy scores tended to have stronger imitative compatibility effects for the object stimulus (correlation was approaching significance). Conversely, in the current experiment, more empathetic participants tended to have stronger imitative compatibility effects for the object initially. However, there was no correlation between empathy and the initial compatibility effects for the object in section 1 of both experiments 5 and 6 (as these conditions were identical between experiments), indicating that no correlation between empathy and initial imitative compatibility effect is present when collapsed across a larger number of participants, giving the comparison more power (*r*(53) = .212, *p* = .127). In addition, it is unlikely that the differences between the two experiments are due to group differences in empathy, as an unpaired t-test between empathy scores for participants in experiment 5 (M = 48.96) and 6 (M = 48.77) indicating that there was no significant difference in empathy scores between the two groups (*t*(40.133) = .059, *p* = .954).

3.3.3.2 No significant effect of belief

In experiment 6, we found no imitative compatibility effects were observed for the object stimulus before or after the belief manipulation. We found that there was no significant interaction between condition and compatibility, indicating the absence of an effect of belief in this experiment.

However, although the imitative compatibility effects did not reach statistical significance, the results indicate a trend towards an effect of belief was present.. However, there was substantial inter-participant variability in compatibility effects and belief effect, with some participants not showing this belief effect at all, thus the belief effect did not reach statistical significance. The main difference between the two experiments is that in experiment 5, the participant observed two additional blocks of trials, in which a real human hand stimulus was observed, followed by the object stimulus again, prior to the belief manipulation. The fact that initial compatibility effects present for the object decreased in the belief condition (experiment 5), where the hand is never observed supports our explanation that seeing a real biological hand stimulus led to an inhibition of the initial imitative compatibility effects for the object, as it appeared comparatively less biological. Conversely, as there were no initial compatibility effects for the object in the current experiment, it is possible in this group of participants there was no initial implicit human belief and having not seen a real human hand, which may have led to the increase in imitative compatibility observed.

As discussed in **section 3.2,** some studies have also shown that prior implicit beliefs of the participant can interfere with the belief effect. For example, as discussed in **section 1.7.3**, it is possible that stimulus an unambiguous ‘non-human’ stimulus such as a robot, may cause participants to form the implicit belief that the stimulus is not human, in spite of any instructions given, leading to ineffectiveness of the belief manipulation (e.g. Press et al., 2005). On the other hand, it may be easier to manipulate belief for an abstract non-biological stimulus, which is more ambiguous, as there may be less of an implicit belief regarding its agency; therefore a modulation of automatic imitation may be more likely to occur (e.g. Stanley et al., 2007). This supports the idea that in experiment 5, participants their implicit belief that the object represented a human hand may have been altered following observation of the real hand hence they were not affected by the belief manipulation. On the other hand, participants in experiment 6 had no initial belief that the object represented a human hand and therefore were more susceptible to the belief manipulation. Interestingly, RTs were significantly faster in the ‘no belief’ condition and were significantly slower in the ‘belief’ condition at all three SOAs. Based on the results of experiments in **chapter 4**, it is likely that the slower RTs could be explained by the increased cognitive demands of mapping one’s own hand onto a rotated stimulus. This is discussed in further detail in **section 4.3.3.3**. Interestingly, as discussed in **section 3.2.4.3**, RTs were actually faster in the belief condition compared to the initial object condition in experiment 5. If the mental rotation of the stimulus caused the effect in the current experiment, this would participants in experiment 5 did not believe that the object represented a human finger movement, hence no mental rotation (causing slower RTs) occurred.

We also investigated whether there were any correlations between imitative compatibility effects and empathy, which might explain the inter-participant variability in terms of the (non-significant) belief effect. There was a positive correlation between empathy scores and belief questionnaire average score, suggesting one of two possibilities. Firstly, participants with high empathy scores were more likely to be influenced by experimental demand effects and respond based on the experimenter's inferred expectations. Secondly, participants with high empathy may have responded truthfully and have actually been more likely to believe the information they have been given in comparison with people with low empathy scores. The fact that the positive correlation between compatibility effects for the object (after belief) at 120ms SOA and empathy scores is also approaching significance supports the latter explanation, and suggests the potential belief effect may have been driven by participants who had a high empathy score. This is therefore a potential source of variability in experiments attempting to manipulate belief regarding the agency of the stimulus.

3.3.3.2 Lack of significant imitative and orthogonal compatibility effects

Another important point for discussion is the lack of significant imitative compatibility effects, in both experiment 5 and 6, due to large error bars and variability of the belief effect between participants. In addition, none of the experiments using the rotated paradigm have suggested an influence of orthogonal spatial compatibility. It will be important to reduce the variability of the data and increase the effect size in future experiments in order to conclusively show that belief modulates automatic imitation effects. In the current experiment, we aimed to determine whether the effect of belief is caused by increased attention or are due to a true effect based on beliefs about stimulus agency. The experiment was therefore designed to separate these two possibilities, by separating automatic imitation (an increase in which would represent a true belief regarding agency in the belief condition) and orthogonal spatial compatibility effects (an increase in which would represent an increase in attention for the object stimulus in the belief condition). However, as in experiment 5, we have not observed any significant effects of orthogonal spatial compatibility, so we do not have a 'baseline' from which to compare the two possibilities. Ideally increasing both orthogonal spatial compatibility for the object, and further increasing imitative compatibility effects, would allow us investigate this further.

3.3.4 Conclusion

In experiment 6, no significant effect of compatibility was present, therefore in contrast to experiment 5, no imitative compatibility effects were observed for the object prior to belief. As in experiment 5, no significant effect of belief was produced. However, while no firm conclusions can be drawn from these results, in contrast to experiment 5, there was a non-significant trend for imitative compatibility in the belief condition that was not present prior to belief.. However, there was a high level of inter-participant variability in the belief effect; therefore the imitative compatibility effects did not reach statistical significance.

Despite the lack of significant compatibility effects, this trend suggests that belief regarding stimulus agency can potentially have an effect on automatic imitation effects. The fact thatno trend towards a belief effect was present in experiment 5 suggests that seeing the observing the hand stimulus may have counteracted the effect of the belief manipulation, making the object appear comparatively less biological. The questionnaire results also suggest that more empathetic individuals may be more susceptible to belief manipulations.

Chapter Four

Do attention and belief modulate imitative compatibility effects?

4.1 Chapter Introduction

Three experiments are presented in Chapter 4, culminating in an improved version of the rotated paradigm, in which imitative compatibility is successful dissociated from all other forms of spatial compatibility.

Initially in **experiment 7**, we further examined whether directing attention to the stimulus movement would increase the strength of the imitative compatibility effects produced, and reduce the significant inter-participant variability in compatibility effects observed in Chapter 3. Additionally, participant's eye movements were tracked in order to investigate whether there would be any correlation between visual fixation/attention on the moving stimulus and imitative compatibility effects.

In addition to the attentional aspect explored in experiment 7, we aimed to further investigate the belief effect. Specifically, we were interested in determining whether a human belief about agency of the observed object influences imitation through a general increase in attention to the stimulus (enhancing spatial compatibility effects), or a true belief effect in which a belief that the non-biological stimulus movement is based on a human movement may upregulate the activity of the MNS facilitating imitative compatibility effects (as discussed in **Section 3.2**). Our previous results support the presence of a belief effect: imitative compatibility effects were present in the group of participants who had seen the hand first in both experiment 1b and in experiment 4. In addition, a non-significant trend of imitative compatibility for the object stimulus was present in the belief condition for experiment 6. However, these imitative compatibility effects did not reach statistical significance or produce any interactions between compatibility and belief, due to variability in compatibility effects between participants. Additionally, there was wide variation in susceptibility to the belief manipulation among participants in experiments 5 and 6, possibly due to individual empathy or personality differences.

In **experiment 8**, we further explored the potential belief effect observed in experiment 6; however the diffuse flash go signal was replaced with the new focused flash to draw attention to stimulus movement in order to increase the size of the imitative compatibility effects. Furthermore, we aimed to eliminate the possibility of a reoccurrence of the unexpected imitative compatibility effect for the object stimulus (prior to the belief manipulation), which occurred in experiment 5. Based on the hypothesis that participants would be unlikely to associate a horizontally set blue rectangle with a moving finger movement/hand, the object stimulus was once again altered in two ways: 1) the larger stationary square part of the object stimulus (which represented the fist of the hand) was removed leaving only the moving rectangle; 2) the colour of the rectangle was altered to pale blue shade as opposed to the previous pale pink/beige, which could more easily be associated with the colour of human flesh (see **Appendix C2**). However, importantly luminance was matched between the previous pink and the new blue objects (see **Appendix C3**). A consistent pattern of results was produced in experiment 7 and 8 suggesting that an additional Simon effect was contributing to the large compatibility effects produced. Therefore, in **experiment 9** the stimuli were presented such that we effectively isolated the imitative component by pitting imitative compatibility against both orthogonal spatial compatibility effects *and* the Simon effect. This allowed us to examine exactly how beliefs regarding agency modulate imitative compatibility effects in the absence of confounding spatial variables.

4.1.1 Experiment 7 - Introduction

A number of lines of evidence suggest that 'selective attention' to stimulus movement is required for the emergence of imitative compatibility effects (Bach et al., 2007; Chong et al., 2008; Gowen et al., 2010). In one's everyday environment far more perceptual information is available than can be effectively processed by the visual system. Due to this high level of clutter in the visual field it is not possible to attend to all areas of a given scene at the same time. For this reason, visual attention is a selective process, whereby the most relevant areas or objects in a scene must be prioritised to order to ensure that the most informative aspects of the scene are processed (Driver and Baylis, 1989).

Models of visual attention attribute eye gaze to be driven by two different sources: 1) simple stimulus features such as contrast, brightness or motion, which drive attention in a bottom-up fashion (e.g. automatic saccades to the unexpected appearance of a stimulus in the periphery); 2) strategic exploration of the stimulus based on prior knowledge, expectations and learned associations in a top-down fashion (e.g. searching for a specific object within a scene). For perception of some stimuli to be suppressed or ignored, all stimuli must be processed to a certain extent during initial 'pre-attentive' processing of low level stimulus features, which occurs rapidly and automatically. Consequently, while prioritised stimuli selected for intensive processing are likely to reach the threshold of awareness (Posner, 1994), others are only processed 'superficially'. The biasing of attentional resources toward the most relevant information in a given situation is known as 'selective visual attention' (Theeuwes, 1993). Eye gaze is predominantly steered by visual attention therefore eye movements may serve as an indicator of visual attention. However it is important to note that uncoupling of eye gaze and visual attention can occur, therefore calling into question the extent to which this relationship is valid.

It is possible that the variability in the experiments presented in Chapters 2-3 is that while some participants may have continued to pay attention to the moving stimulus, the diffuse nature of the yellow flash go signal used allows for the possibility that some participants may alternatively focus on the more peripheral areas of the screen to detect the yellow flash, thus ignoring the movement of the stimulus altogether (as it is not a requirement of the task to attend to the movement of the stimulus, and could even be seen as a 'distraction'). We therefore hypothesized that the diffuse yellow flash go signal used in experiments 1-6 may have drawn some participants' attention away from the movement of the stimulus, reducing the overall strength of the compatibility effects produced. Furthermore, individual variation in the amount of selective attention paid to the moving stimulus may be a contributing factor to the wide inter-participant variability in compatibility effects observed in Chapter 3. A wider focus of attention may increasingly become an issue later in the experiment, when many trials presenting the same stimulus have already been completed, thus stimulus movement may fail to automatically capture attention, or the participant's attentional strategy may change as they may regard irrelevant movement of the stimulus as unimportant or even distracting to the task of detecting the diffuse yellow flash. For example, experiment 4, which was a particularly long experiment consisting of 4 parts, imitative compatibility effects decreased as the experiment went on, which could be explained in part by reduced attention to the stimulus movement.

Based on the fact motion in the visual field carries salient information for the observer in one's daily life (for example, avoiding collisions with approaching people/cars), coupled with the fact that the human visual system is known to have specialized motion processing capabilities one might assume that motion automatically captures attention. However, studies which have examined the attentional capture by moving objects indicate that it is not motion per se that captures attention; rather, studies suggest that it is the sudden onset of motion that captures attention (Abrams and Christ, 2003; Franconeri and Simons, 2003). For example, it has been observed that a continuously moving target was not easier to find in a visual search task; however a motion onset target was easier (Abrams and Christ, 2003). A number of other groups have replicated the finding that the sudden onset of movement (Yantis and Jonides, 1990), as well as stimuli that appear to be 'looming' towards the observer (Franconeri and Simons, 2003) appear to automatically capture attention in a bottom-up fashion. They suggested reasoning behind this observation is that continuous motion is too common an event in our everyday environment to automatically capture attention, whereas the sudden onset of a motion could be informative of behaviourally urgent events (Abrams and Christ, 2003). It has been argued that the human visual system may be evolutionarily attuned to sudden movement/looming stimuli, as such stimuli require an immediate behavioural response for survival purposes (Franconeri and Simons, 2003). However, there is some debate as to whether or not attentional capture by abrupt movement onsets is truly 'automatic' based on evidence that attentional capture by abrupt onsets depends on the top-down attentional control set of the observer (Folk et al., 1992). In Folk et al.'s paradigm, they found that when a search target was defined in terms of colour, an irrelevant motion cue failed to capture attention, suggesting it is possible to ignore movement onsets in circumstances where the irrelevant motion cue does not possess the feature the participant is searching for. However, in their experiment the irrelevant motion cue was presented 150ms prior to the target. When this paradigm was adapted, such that the abrupt onset distractor stimulus was presented simultaneously with the target, search times increased suggesting the movement onset of the distractor automatically captured attention (Schreij et al., 2008). However, Folk and Remington (1998) countered that the onset related costs could be to do with 'non-spatial filtering' mechanisms, as described by Kahneman et al.

(1983), who observed longer response times to a target when distractor objects appeared simultaneously with the target. Folk and Remington, (1998) suggest that simultaneously appearing distractors compete for attention and need to be filtered out i.e. there is no attentional capture of the distractor, but the 'filtering out' mechanism could account for the delay in detecting the target. However, it has been suggested that such attentional capture is only 'partially' automatic, as it has been demonstrated that abrupt onsets do not necessarily capture attention against one's own intentions i.e. when attention is highly focused on another task (Yantis and Jonides, 1990). Based on this finding they suggested that the visual system gives high priority to abrupt onsets when in a diffuse attention mode, however when attention is highly focused on another task, less priority is given to the potentially distracting abrupt onset stimulus. In a diffuse attention mode, the abrupt onset of the flash may be given higher priority than the moving finger. Consequently, we predicted that the focus of attention may be wider for the diffuse flash thus the task-irrelevant stimulus movement may receive less attention relative to the task-relevant yellow flash. On the other hand, we predicted that for the focused flash participant's attention would be narrowly focused on the area in which stimulus movement occurs as this coincides with the location of the focused flash. With this in mind, in experiment 7, we aimed to increase the size, and decrease the overall variability of imitative compatibility effects produced, by biasing selective attention toward the movement of the stimulus using a smaller rectangular shaped focused flash go signal that appeared in the area in which stimulus movement occurred. Only the hand stimulus was presented in the experiment. Participants responded to the usual diffuse yellow flash go signal for half of the experiment and responded to the smaller focused yellow flash for the other half of the experiment. We aimed to compare participant's compatibility effects for the diffuse flash with the new focused flash. We predicted that in the focused flash condition there would be a narrow focus of attention on stimulus movement, and thus compatibility effects would be stronger relative to the diffuse flash condition where the focus of attention may be wider. In addition, we wanted to examine whether or not the order in which the flashes were presented would affect the participant's attentional strategy.

Additionally, the participant's eye movements were tracked using a table mounted eye tracker in order to investigate whether there would be any correlation between visual attention to the moving stimulus and imitative compatibility effects. Eye movements have been used by a number of groups a measure of the locus of attention, since direction of gaze is generally considered to be tightly coupled to the orienting of attention (Hoffman and Subramaniam, 1995; Deubel and Schneider, 1996). We aimed to compare eye tacking data between the diffuse and focused flash conditions, and look at individual differences in eye behaviour. We hypothesized that in the diffuse flash condition, eye movements would show a wider distribution of fixations in locations outside of the region of the stimulus movement, indicating a wider focus of attention; whereas in the focused flash condition, there would be a narrow focus of attention indicated by more fixations on the area in which stimulus movement occurred.

4.1.2 Methods

4.1.2.1 Participants

20 right-handed healthy individuals were recruited for the study; however, one participant's data was excluded from analysis due to not complying with the instructions (responding incorrectly by releasing instead of pressing in one of the blocks). The mean (±SD) age of the remaining 19 participants (9 female) was 22.11 (±3.01) years. The mean (±SD) laterality quotient was 88.83 (±15.79). The study consisted of a single testing session lasting approximately 90 minutes, and participants were paid £7.50 for their participation.

4.1.2.2 Design and procedure

Participants observed the same series of images of a human hand rotated 90 degrees counter-clockwise executing upwards or downwards movements of the right index finger as in Chapter 3. The experiment consisted of two sections. Participants responded to the usual diffuse yellow flash go signal for one section of the experiment, and responded to the new focused rectangular yellow flash for the other section of the experiment. The rectangular yellow flash go signal appeared in the location of the moving finger, and covered the full area in which the finger movement occurred in both directions (upwards and downwards). The order of presentation of each flash type (diffuse flash vs. focused flash) was counterbalanced between participants. Participants completed a short questionnaire following each section of the experiment, which was designed as a self-reported measure of which flash (focused or diffuse) participants felt focussed their attention on the movement of the finger the most.

4.1.3 Results

4.1.3.1 Analysis of error data

The same exclusion criterion used in previous experiments was applied. This resulted in a total loss of 1.39% of trials on average for the diffuse flash, and 1.55% of trials for the focused flash. In addition the same error types (described in experiment 1a) could be incurred in this experiment.

Overall, participants made a low level of errors **(Table 22 and Table 23)**; therefore no individual participant's data was removed.

Table 22: Mean % Anticipation errors, no-go errors and second response errors calculated as a percentage of the total number of trials where the error could occur for each type of error overall across the experiment.

Type of Error (total number of trials where error could occur)	**Diffuse Flash Mean % Errors (± SE)**	**Focused Flash Mean % Errors (± SE)**	**Overall Mean % Errors (± SE)**
Anticipation Error (336)	0.38 (± 0.13)	0.62 (± 0.19)	1.00 (± 0.31)
No-go Error (48)	0.03 (± 0.01)	0.01 (± 0.00)	0.02 (± 0.01)
Second response error (336)	0.00 (± 0.00)	0.00 (± 0.00)	0.00 (± 0.00)

Table 23: Mean % no-go and anticipation errors (± SE) for each flash type. No-go errors were made out of a potential 48 and anticipation errors were made out of a potential 336. **Bold** type represents compatible trials.

Stimulus	**Mean % No-go errors (± SE)**	**Mean % Anticipation errors (± SE)**
Diffuse flash	**1.10 (± 0.49)** 1.43 (± 0.39)	**0.23 (± 0.10)** 0.14 (± 0.06)
Focused flash	**0.44 (± 0.20)** 1.32 (± 0.33)	**0.23 (± 0.08)** 2.63 (± 0.81)

4.1.3.2 Analysis of reaction time data

Overall mean RTs (ms) (±SE) are presented in **Table 24**. Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects.

Table 24: Mean RTs (ms) (± SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (*p* < .05).

Stimulus	**Response**	**SOA (ms)**	**Mean RT (ms) ± SE**
Diffuse flash	Press	0	**329.57 (± 85.65)** 330.86 (± 86.32)
		120	**294.27 (± 67.83)** 299.24 (± 74.73)
		280	**267.68 (± 61.29)** 292.27 (± 59.58)*
	Release	0	**327.24 (± 68.38)** 338.52 (± 68.13)
		120	**297.78 (± 46.80)** 292.46 (± 65.64)
		280	**290.02 (± 43.90)** 281.05 (± 60.36)
Focused flash	Press	0	**333.73 (± 61.53)** 333.81 (± 61.16)
		120	**286.25 (± 55.07)** 297.25 (± 49.36)
		280	**271.48 (± 41.28)** 297.48 (± 34.77)*
	Release	0	**297.04 (± 57.36)** 321.61 (± 57.36)
		120	**330.09 (± 53.61)** 284.68 (± 40.89)*
		280	**288.23 (± 27.86)** 271.18 (± 37.12)*

A mixed design (2x3x2x2) repeated measures ANOVA was conducted, with response type (press/release) x SOA (0, 120, 280) x compatibility (compatible/incompatible) x flash (large diffuse flash/small focused flash) as within-subjects factors. There were a number of interactions with response type, including a significant interaction between response, SOA and compatibility; therefore, mean RTs for press and release response were analysed separately.

Two repeated-measures ANOVAs were therefore conducted on participants' mean RTs with flash x SOA x compatibility for each flash (large flash/small flash) with starting flash (diffuse first vs. focused first) as a between subjects factor for pressing and releasing responses. Starting flash was included as a between-subjects factor in order to investigate whether any order effects would be present from seeing either the diffuse flash or focused flash first. The usual significant main effect of SOA was present for both of the ANOVAs.

For pressing responses, there was a main effect of compatibility (*F*(1,17) = 37.00, p = .000) indicating compatible responses (M = 297.24ms) were significantly faster than incompatible responses (M = 308.41ms). There was a significant interaction between compatibility and starting flash (*F*(1,17) = .4.445, *p* = .050). An unpaired t-test revealed that compatibility effects were significantly greater for the focused flash first group (M = 15.40ms) compared to the diffuse flash first group (M = 7.37ms) (t(17) = -2.108, p = .050). There was also a significant two-way interaction between SOA and compatibility (*F*(2,34) = 9.672, *p* = .000). There was a significant three way interaction between SOA, compatibility and starting flash was approaching significance (*F*(2,34) = 3.141, *p* = .056). Unpaired t-tests revealed that compatibility effects were stronger for the focused first group compared to the diffuse first group at 280ms (*t*(17) = -2.872, *p* =.011); however there was no significant difference between groups at 0ms or 120ms **(Figure 53c)**.

For releasing responses there was a significant interaction between SOA and compatibility (*F*(2,34) = 5.253, *p* = .010), indicating that compatibility effects were significantly stronger at 0ms (M = 9.88ms) compared to 280ms (M = -13.12ms) (t(18 = 2.804, p = .012); and compatibility effects were significantly stronger at 120ms (M = 3.11ms) compared to 280ms (M = -13.12ms) (*t*(18) = 2.582, *p* = .019). However, there was no significant difference in compatibility effects at 0ms (M = 9.88ms) compared to 120ms (M = 3.11ms) (*t*(18) = .793, *p* = .012). In addition, the interaction between SOA, compatibility and starting flash was approaching significance (*F*(2,34) = 3.022, *p* = .062). Unpaired t-tests revealed that compatibility effects were stronger at for the focused first group (M = 18.08ms) compared to the diffuse flash first group (M = 2.49ms) at 0ms (*t*(17) = -2.137, *p* = .047), but not at 120ms or 280ms **(Figure 53d)**.

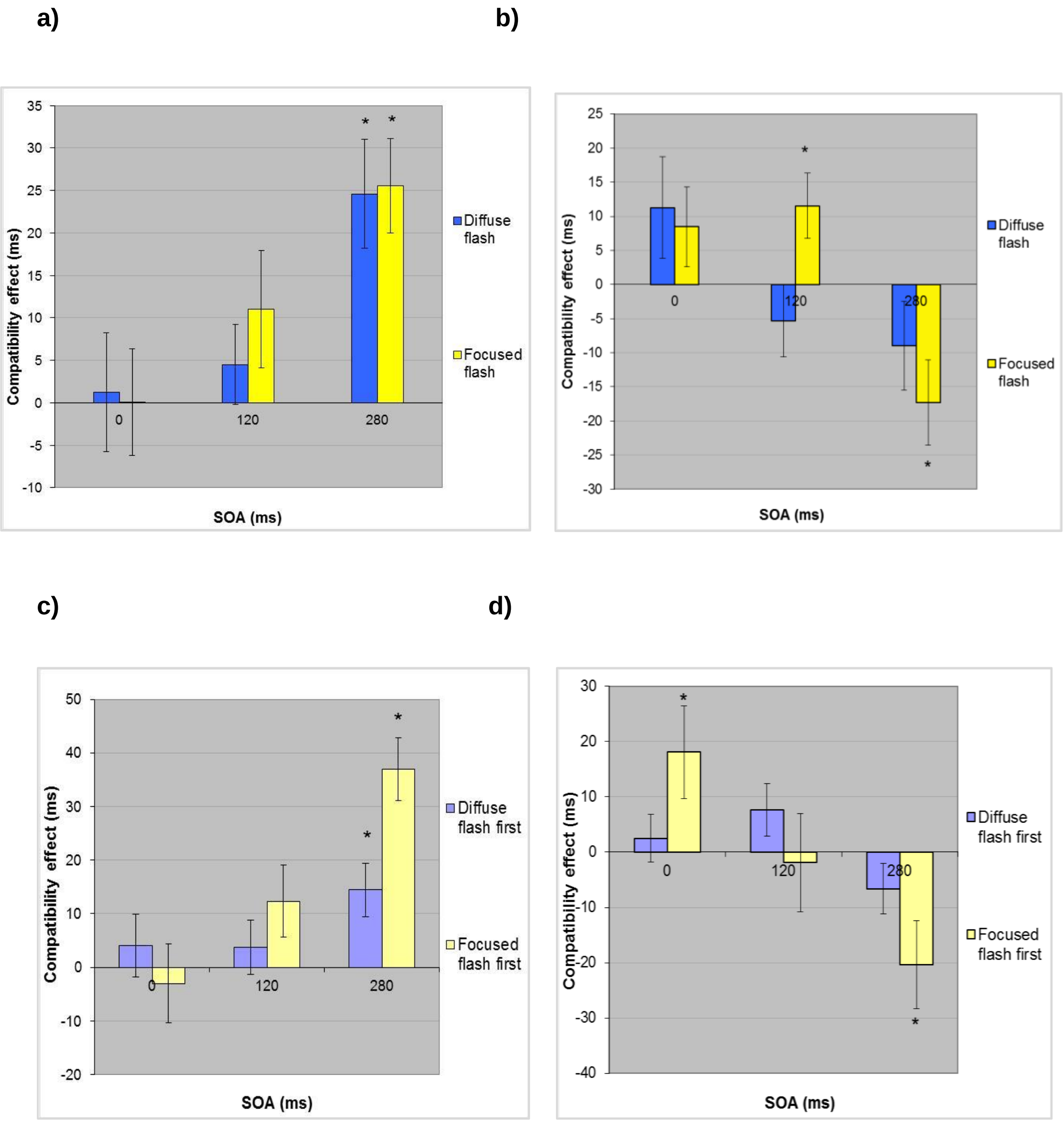


Figure 53: a) Mean compatibility effects for pressing responses for the diffuse and focused flash across SOAs; **b)** Mean compatibility effects for releasing responses for the diffuse and focused flash across SOAs; **c)** Mean compatibility effects for pressing responses averaged across both focused and diffuse flashes for diffuse flash first group and focused flash first group; **d)** Mean compatibility effects for releasing responses averaged across both focused and diffuse flashes for diffuse flash first group and focused flash first group

4.1.3.3 Analysis of eye tracking data

Eye tracking data was collected for 16 out of the 19 participants using an ASL Eye-Trac 600 table mounted eye tracker. Three 'areas of interest' were identified: 1) the finger (where movement takes place), 2) the rest of the hand and 3) outside of those areas. The eye tracking data was used to calculate the percentage of time looking in each of these three areas of interest during the diffuse flash condition and the focused flash condition. Initial results across the 16 participants showed a 3% mean increase in the percentage of time spent looking at the finger and a 5% increase in percentage of time looking at the hand for in the focused flash condition compared to the diffuse flash condition. Although the expected increase for the focused flash was present, the difference between mean % time spent looking at the finger in the focused vs. diffuse flash was not significantly different overall. However, due to the significant interactions with starting flash in the RT analysis, the participants were further split into two groups: those who saw the focused flash first and the diffuse flash second (focused flash first group), and those who saw the diffuse flash first and the focused flash second (diffuse flash first group).

The difference between the percentage of time spent looking at the finger for the diffuse (M = 17) vs. focused flash (M = 26) in the diffuse flash first group was approaching significance (*t*(7) = 2.216, *p* = .062); they tended to spend more time spent looking at the finger for the focused flash compared to diffuse flash **(Figure 54)**. However, in the focused flash first group there was no significant difference between the percentage of time looking at the finger for the diffuse (M = 20) vs. focused (M = 23) flash (*t*(6) =.685; *p* =.519) **(Figure 54)**.

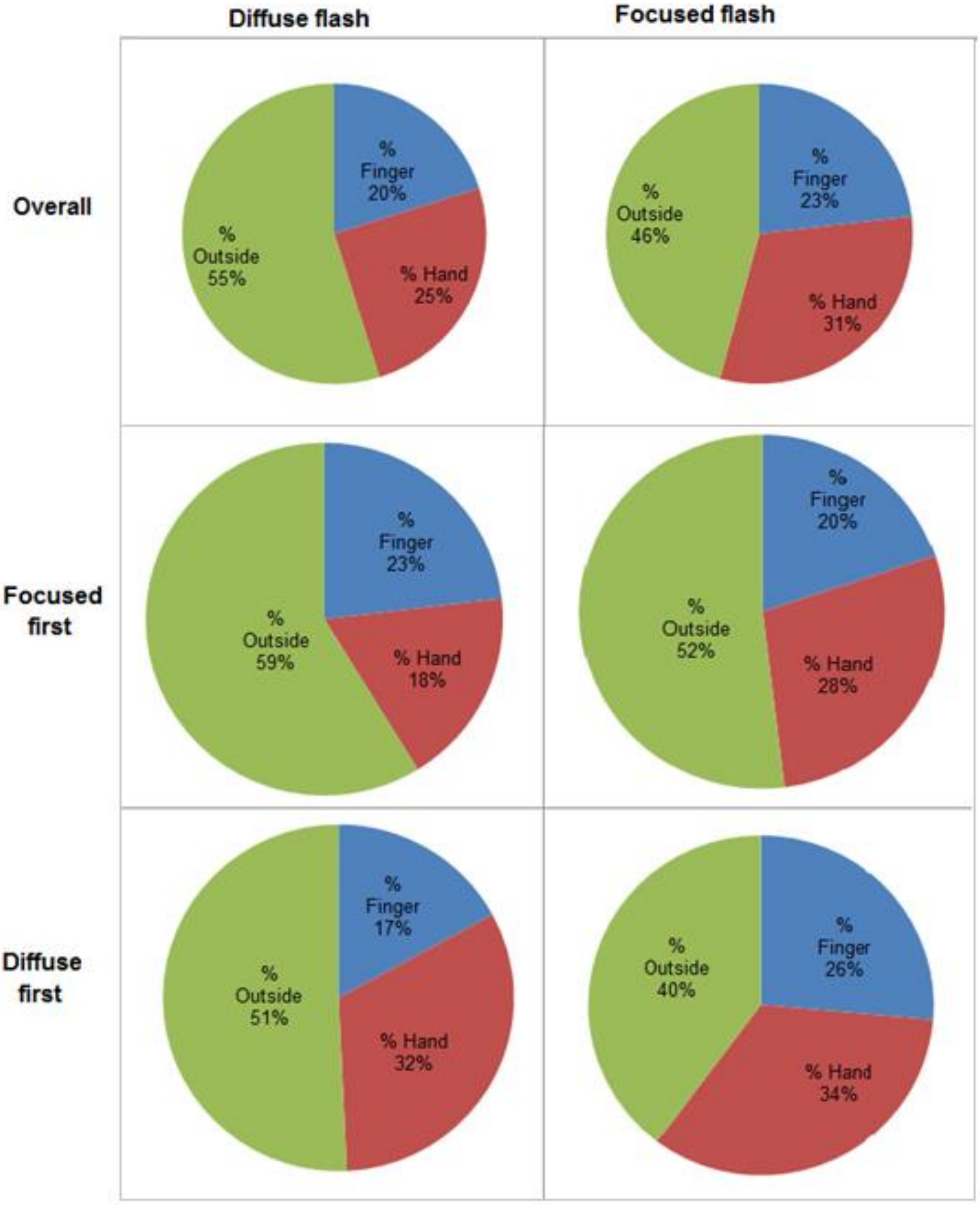


Figure 54: % of time looking at each area of interest: **a)** overall for the diffuse flash; **b)** overall for the focused flash; **c)** for the diffuse flash in the diffuse flash first group; **d)** for the focused flash in the diffuse flash first group; **e)** for the diffuse flash in the focused flash first group; **f)** focused flash in the focused flash first group

Pearson's correlation tests were conducted to determine whether there was a significant correlation between size of imitative compatibility effects and the % of time looking at the moving finger. The large compatibility effects at 280ms, which go in opposite directions for pressing (positive compatibility effect) and releasing (negative compatibility effect) responses suggested that imitative compatibility effects at this time point may be contaminated with an additional Simon effect due to the focused flash drawing further attention to leftwards/rightward movement of the stimulus (discussed in further detail in the discussion section of experiment 8 - **Section 4.2.4.1**). For this reason, we chose to look at the 0ms (release) compatibility effects, as this time point shows a significant imitative compatibility effect for the focused first group, which occurs early in the movement, so was less likely to be contaminated with the Simon effect **(Figure 53a and 53b)**.

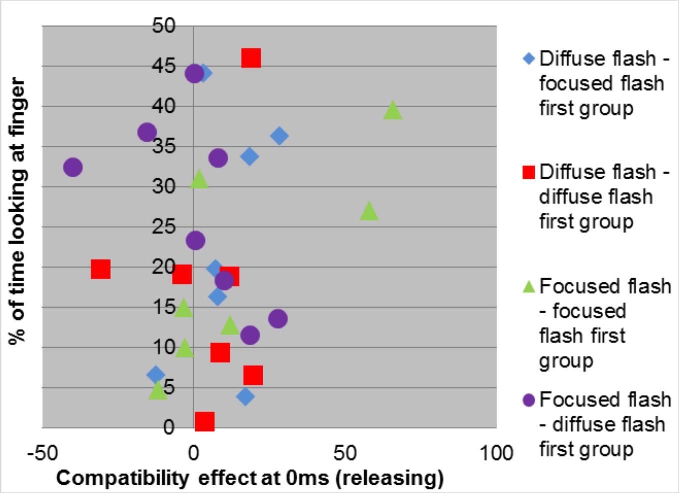


Figure 55: Scatter graph of correlations between percentage of time looking at finger and 0ms releasing compatibility effects for each group and flash

A Pearson's correlation test were conducted between the imitative compatibility effect at 0ms (release) in the focused first group and diffuse first groups (averaged across the focused and diffuse flashes), and % of time looking at the finger stimulus. There was a significant positive correlation between time looking at the finger and compatibility effects and % of time looking at the finger (averaged across the focused and the diffuse flash) (r(7) = .786, *p* = .036) **(Figure 55 and 56a)**. However there was no significant correlation between imitative compatibility effects and % of time looking at the finger in the diffuse first group (*r*(8) = -.296, *p* = .476). There was also a significant correlation between compatibility effects in the focused first group for the focused flash (r(7) = .772, p = .042) **(Figure 55 and 56b)**. None of the other correlations reached statistical significance (p > .122).

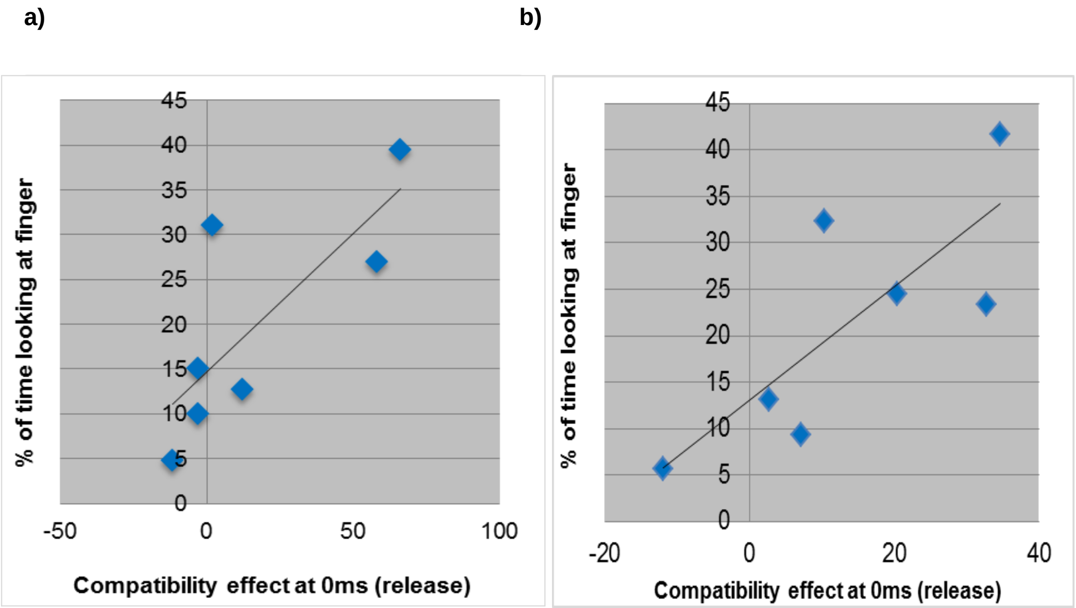


Figure 56: a) Positive correlation between 0ms releasing compatibility effects and % of time looking at the finger for focused first group (averaged cross flashes); **b)** positive correlation between 0ms releasing compatibility effects and % of time looking at the finger for focused first group for the focused flash.

4.1.3.4 Analysis of questionnaire data

Mean questionnaire scores for self-reported attention questionnaire scores are presented in **Table 25**. Paired t-tests between questionnaire responses for the diffuse flash vs. the focused flash were conducted. The difference between responses for question 2 ‘how much attention were you paying to the fist of the hand (the rest of the hand excluding the moving index finger’ condition were higher on average for the diffuse flash (M = 2.16) than for the focused flash condition (M = 1.79) was approaching significance (t(18) = 1.944, p = .068). No other significant differences were found; however, in the questionnaire at the end of the experiment, participants were asked which flash they felt focused their attention more on the movement of the finger, and the majority (12 out of the 19) of participants felt that the focused flash focused their attention more on the movement of the finger. Only 3 participants felt the diffuse flash focused their attention on the movement of the finger more, and 4 participants felt that there was no difference in their attention.

Table 25: Mean attention questionnaire scores for the diffuse flash and focused flash. A score of 10 represents 'very much'; a score of 5 represents 'to some extent' and a score of 0 represents 'not at all'.

Q. No	**Question**	**Mean score-Diffuse flash**	**Mean score-Focused flash**
1.1	How much attention were you paying to the moving index finger?	5.14	6.09
1.2	How much attention were you paying to the fist of the hand (the rest of the hand excluding the moving index finger)?	2.41	1.39
1.3	How much attention were you paying to areas of the screen outside of the image of the hand and moving finger?	2.16	1.79
1.4	How much attention were you paying to the direction of the movement of the finger (up or down)?	4.14	4.28
1.5	How much did you feel that the movement of the finger made you want to move your own finger?	5.28	5.15
2.1	Do you think you paid more or less attention to the movement of the finger when the flash was constricted to the area with the small flash?	6.07	6.65
2.2	Please indicate (circle) which flash you feel was more successful in focusing your attention on the movement of the finger: a) the small flash b) the large flash c) no difference	a) Focused (small) flash = 12 participants b) Diffuse (large) flash = 3 participants c) No difference = 4 participants	

4.1.4 Discussion

The current results suggest that, as hypothesized, the focused flash go signal focused participant's selective visual attention on the finger movement, and this caused large imitative compatibility effects to be present for the focused flash at 280ms (pressing) and 120ms (releasing). However, a large negative compatibility effect was also present for at 280ms (releasing) for the diffuse flash. Therefore, interestingly, there was not an overall main effect of flash type, but rather an overall effect of 'starting flash', indicating that strong compatibility effects were present in the focused flash first group (regardless of flash type observed), suggesting that seeing the focused flash initially biased selective attention towards stimulus movement, and this bias carried over to the diffuse flash condition. When split into groups according to starting flash, again there are more significant compatibility effects for the focused first group (280ms (pressing response), 0ms (releasing response), 280ms (pressing response) compared to the diffuse first group (280ms pressing response). Again, only in the focused first group is a compatibility effect present at 0ms SOA for the releasing response. These results suggest that the order in which the flash types (focused vs. diffuse flash) were presented directly affected attention and performance. In the group of participants who saw the diffuse flash first, as expected, imitative compatibility effects were weaker for the diffuse flash and then increased in the focused flash condition where attention was more focused on stimulus movement. However, in the group of participants who saw the focused flash first, large compatibility effects of approximately equal size were present for both the focused and diffuse flashes. This suggests that a carry-over effect or 'training effect' occurred in the focused flash first group whereby seeing the focused flash first causes an initial increase the focus/bias towards the finger movement, and this bias carried over to the diffuse flash condition.

This finding seems to fit in well with the idea that a 'top-down attentional set' (Wolfe and Horowitz, 2004) or attentional strategy, in which attention is selectively biased towards the most informative object or part of a scene based on prior knowledge or task demands. In theory, when task demands change an observer should switch their attentional set/strategy in accordance with the new task demands. However, it has been observed that an original attentional strategy may carry-over from a previous task to a second task, thereby influencing attention (and performance) in the second task (Leber and Egeth, 2006). In this experiment, in the focused flash first group, seeing the focused flash appears to have initially biased attention towards the stimulus movement as this is the most informative area based on task demands (responding to the focused flash which appeared in this area), and this attentional set appears to have carried over to the second part of the experiment in which the diffuse flash was the go signal. Several groups of researchers have shown that selective attention is often directed to items and locations that were previously relevant (Maljkovic and Nakayama, 1994, 2000); supporting the hypothesis that allocation of attention can be influenced by past experience. These findings also fit in well with the idea that attention is guided by 'spatial priors'. Spatial priors are prior knowledge about the location of objects or relevant information in a scene due to previous experience of observing the scene. For example, it had been found that observers naturally tend to initially fixate in the centre of a scene before making eye movements to other areas (Tatler, 2007). This appears to occur based on bottom-up influences (independently of task demands or stimuli), and may be due to the fact the centre is most informative, or is the ideal place to begin a search. However, Einhäuser et al. (2008) posit that while attention may initially be allocated based on bottom-up influences the first time one observes a scene, top-down spatial priors (dependant on task demands) may affect the allocation of attention on subsequent viewings. Our findings suggest that 'automatic imitation' is modulated by the top-down selective attention. One possibility is that the focused flash could implicitly lead participants to regard the moving finger as an important aspect of the scene to be prioritised once their attention had been drawn to it in the initial focused flash condition. Therefore participants may have maintained the same attentional strategy of a narrow focus of attention on stimulus movement in the diffuse flash condition, rather than adopting a wider spread of attention. Observing the diffuse flash first, on the other hand, may lead participants to conversely regard the stimulus movement as unimportant or distracting to the task of detecting the yellow flash, causing participant's to pay less attention to stimulus movement. This fits in with the idea that movement onset does not necessarily capture attention against the observer's intentions e.g. even when they are highly focused on another stimulus (Yantis and Jonides, 1990). Only in the diffuse flash condition is the onset of movement potentially 'distracting', therefore attention may have been less focused on stimulus movement.

These findings are contrary to the notion that imitative compatibility is an automatic process, and suggest that the level of imitative compatibility produced is modulated by selective visual attention to stimulus movement. This also supports previous research suggesting that visual attention to stimulus movement is crucial for the emergence of imitative compatibility effects (Bach et al., 2007; Chong et al., 2009).

The current findings are also interesting in terms of the ongoing debate regarding whether or not the onset of movement automatically captures attention. Our results show that the amount of imitative compatibility is reduced when participants see the diffuse flash first. This suggests that the diffuse flash trains participants to maintain a wide spread of attention, thus less attention is focused on the movement itself, leading to reduced imitative compatibility effects. On the other hand in the focused first group, seeing the focused flash first trains participants to focus on the movement of the stimuli. These findings indicate that while the simultaneous onset of movement does capture attention; the strength of attentional capture is contingent on the width of the participant's attentional focus. A wide focus reduces attention and therefore imitative compatibility whereas a narrow focus increases attention and imitative compatibility effects. As discussed in **section 4.1.1**, Folk et al., (1992) suggested that a top-down attentional set can eliminate attentional capture by salient distractors presented 150ms prior to the target if they do not share the target feature; however Schreij et al., (2008) found that when abrupt onset distractors appeared simultaneously with the target, they did capture attention. Schreij et al interpreted this such that abrupt onsets do automatically capture attention, whereas Folk et al. (1992) suggested their results could be interpreted in terms 'non-spatial filtering operations'. The current findings, in which the flash appeared simultaneously with the onset of movement, or just after, are in line with Scheij et al. (2008) interpretation as while the current paradigm differs in that the abrupt onset is a human finger movement, the fact that even when participants had a wider attentional focus (diffuse flash first group) some imitative compatibility were present, suggests that the irrelevant movement of the finger stimulus was not 'filtered out' (as suggested by Folk and colleagues) and did capture attention; however, to a lesser extent than in the focused flash first condition which trained participants to have a narrow focus of attention on stimulus movement. This suggests the abrupt onset of movement captures attention, but the extent of attentional capture can be modulated by a 'diffuse' or 'focused' top-down attentional set.

One unexpected finding was a consistently large positive compatibility effect for pressing at 280ms, and a large negative compatibility effect in the opposite direction for the releasing response at 280ms. It is possible that the discrepancy between pressing and releasing responses at 280ms could be explained by the Simon effect (see **section 1.6.1**). Due to the fact that participants are using their right hand to respond, RTs would be faster when the finger moves downwards (rightward movement direction), and RTs are slower when the finger moves upwards (leftwards movement direction). When pressing the button the advantage for the rightward movement caused by the Simon effect would be compatible with the imitative compatibility effect (i.e. participants pressing the button is compatible with the finger moving down - which is also a rightwards movement direction). Thus, for the pressing response, a combination of imitative compatibility and the Simon effect may contribute to the large positive compatibility effect for 280ms. When releasing the button, however, participants would still be responding faster when the finger moves downwards (in a rightward movement direction) due to the Simon effect as they are still using their right hand to respond. However the releasing response would be imitatively incompatible with the finger moving downwards i.e. a rightward movement direction. Thus, for the releasing response, the Simon effect would be operating in the opposite direction to imitative compatibility effect putting the effects in competition, and it appears that the Simon effect is stronger than the imitative compatibility at the 280ms SOA. This could explain why there are no compatibility effects in the releasing condition and at 280ms SOA these effects tend to go in the opposite direction creating a negative compatibility effect.

However, for the focused flash an earlier imitative compatibility effect is also present at 120ms (releasing), which may be less likely to be contaminated by the Simon effect, thus may be more of a true representation of an imitative compatibility effect. The fact that the effect is present for the releasing response also suggests it is an imitative compatibility effect as the Simon effect would be present in the opposite direction to imitative compatibility for releasing. This Simon effect is discussed in further detail in **section 4.2.3.2.**

4.1.4.1 Eye tracking findings

The percentage of time looking at the finger was lower for the diffuse flash compared to the focused flash, suggesting that, as predicted, using a diffuse flash draws some attention away from the movement of the finger (leading to variable compatibility effects). However, the difference was between percentage of time looking at the finger for the diffuse and focused flash was approaching statistical significance only in the diffuse flash first group (due to the carry-over effect in the focused first group). Furthermore, the eye data suggests that seeing the focused flash first increases imitative compatibility, possibly by increasing visual attention to the movement of the finger (via fixation). This is indicated by the fact that individual imitative compatibility effects at 0ms (release) were positively correlated with % of time looking at the finger. However, in the diffuse first group, the results suggest that imitation and visual fixation were dissociated. One possibility to explain this dissociation is as discussed the diffuse flash might place less priority on the movement of the finger and create a wider zone of attention. Therefore even when they are fixating on the finger, it is possible that their focal attention is actually on detecting the yellow flash and not on the stimulus movement. In contrast, in the focused flash first condition may create a narrow zone of attention on stimulus movement as this coincides with the area in which the yellow flash is presented. However, it should be noted that since the eye tracking data is based on the data of 16 participants, thus when split into starting flash group for the diffuse vs. focused flash, the groups are individually very low. It is therefore difficult to form any solid conclusions from this data, and more participants would be needed to test these conclusions further.

4.1.4.2 Questionnaire findings

We found that questionnaire responses for the diffuse flash vs. the focused flashes were conducted (overall, and split into groups according to starting flash) were not significantly different for the focused vs. diffused flash, and the participants scored both flashes similarly. In one respect a lack of difference in scores between the flashes may in part reflect the carry-over effect from the focused flash first group, leading to equally strong imitation for both flashes. However, we might have expected to see a difference in the diffuse flash first group where attention increased for the focused flash compared to the diffuse flash. It is possible that the amount of attention participants paid to the stimulus may not be something participants could correctly introspect about. The short questionnaire completed at the end of the experiment, asking directly which flash the participants felt focused their attention more on the finger may therefore shed more light on the effects of the new focused flash. The majority (12 out of the 19) of participants felt that the focused flash focused their attention more on the movement of the finger. Only 3 participants felt the diffuse flash focused their attention on the movement of the finger more. 4 participants felt that there was no difference in their attention

4.1.5 Conclusion

The results of this experiment suggest that constraining visual attention to the area in which stimulus movement occurs, by using a smaller focused go signal increased imitative compatibility effects. In addition, we observed that there was a carry-over effect in the group who saw the focused flash first, as participants in this group also had a large imitative compatibility in the diffuse flash condition, suggesting seeing the focused flash initially ‘trained’ them to pay attention to the stimulus movement. Finally, imitative compatibility effects were likely to be contaminated by the Simon effect.

4.2 Experiment 8 - Introduction

Based on the results of experiment 7, we hypothesized that imitative compatibility effects would be stronger and less variable when using the focused flash as a go signal. Therefore, in experiment 8, we once again examined the role of belief in modulating imitative compatibility effect, in the same way as we have done in experiments 5 and 6, using the focused flash instead of the diffuse flash. If, as hypothesized, an effect of belief is present we would expect to see an interaction between condition and compatibility. As explained in **section 3.2**, we aimed to determine whether the 'attentional hypothesis' or 'true belief' explanation was correct in terms of interpreting the effect of belief on imitative compatibility effects which has been documented in previous studies (Liepelt and Brass, 2010; Stanley et al., 2007). As in experiment 6, we presented the object stimulus, followed by the object stimulus (with manipulated belief). At the end of the experiment we also presented the hand stimulus to provide a comparison.

In addition, two changes were made in order to remove any possibility of participants initially believing the object may represent a hand or finger. Only the moving rectangle part of the object stimulus was presented in this experiment, and the stationary square part of the object was removed to avoid the possibility of participants associating the object with a hand prior to the belief manipulation. Secondly, the colour of the moving object was changed from flesh coloured pale pink to pale blue. As a blue moving rectangle is a relatively ambiguous stimulus, we hypothesized it would be plausible to believe that the movement of the rectangle could be created based on a human generated finger movement. We hypothesized that we would obtain a dissociation between imitative compatibility effects (shown by a positive compatibility effect) and orthogonal spatial compatibility (shown by a negative compatibility effect). We expected orthogonal spatial compatibility to be present in the initial object condition (but no imitative compatibility should be present as the object is initially associated with a left/right movement). In the belief condition we hypothesized that there would be an increase in orthogonal spatial compatibility if the belief effect represented increased attention following the belief manipulation; or an imitative compatibility effect present for the object in the belief condition if the belief effect represented a 'true belief' effect. We would expect imitative compatibility to be present for the hand stimulus.

4.2.1 Methods

4.2.1.1 Participants

20 right-handed healthy individuals (9 female), with a mean (±SD) age of 21.16 (± 2.48) years were recruited. The mean (±SD) laterality quotient was 93.34 (±11.71). The study consisted of a single testing session lasting approximately 90 minutes, and participants were paid £7.50 for their participation.

4.2.1.2 Design and procedure

Participants observed a series of images of a pale blue rectangle presented in quick succession, therefore appearing to move in a leftwards or rightwards direction. The luminance of the size, shape pale blue object was matched that of the pale pink moving rectangular object shown in previous experiments, and the maximum luminance for the hand (which varied in luminance when tested in different areas) (see **Figure 57** and **Appendix C2 and C3**).

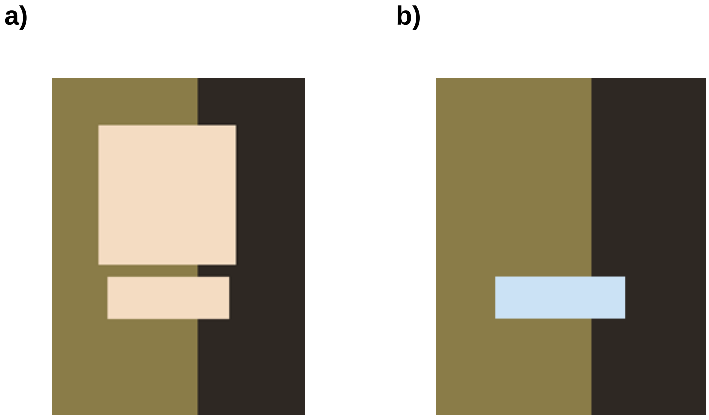


Figure 57: Single frame of: **a)** old version of object stimulus used in experiments 5 and 6; **b)** new pale blue object stimulus

In the object condition (section 1)**,** participants performed the usual automatic imitation paradigm, responding to the new focused yellow flash go signal. The object was referred to as ‘the rectangle’ during this part of the experiment, with reference made to the movement direction being ‘leftwards/rightwards’ in the instructions. The rectangular yellow flash was designed to be large enough cover the whole area in which the finger moved in both directions (upwards and downwards). Prior to the belief condition (section 2) of the experiment, participants completed a short questionnaire probing whether or not they had thought that the rectangle in any way made them think of a human finger movement. They were told that the rectangle movements were actually created using human upward and downward finger movements. It was clearly explained to them the way in which the hand was rotated (demonstrated using the experimenters own hand) and participants shown a printed static image of the hand. Therefore the way the hand was orientated and the direction of movement (upwards=rightwards; downwards = leftward) was made clear to the participants. Participants then completed the belief condition (section 2) viewing the pale blue rectangle stimulus again. In the belief condition, the rectangular object was referred to as ‘the finger’, with reference to the movement direction being ‘upwards/downwards’. Following the belief condition, participants completed a second short ‘belief’ questionnaire**,** as a self-reported measure of the extent to which participants believed that the object movement was based on a human finger movement. In the finger condition (section 3) participants completed the automatic imitation task again whilst viewing the human hand stimulus, in order to provide a comparison with the object and belief conditions. Participants starting response (press or release) was counterbalanced across participants. A short break was given every 48 trials. There were 4 blocks of 48 (4 x 48 = 192) trials in each of the three sections of the experiment (192 x 3 = 576) making up the total of 576 trials. Participants also completed the ELI, EQ2 and AQ questionnaires.

4.2.2 Results

4.2.2.1 Analysis of error data

The same exclusion criterion used in previous experiments was applied. This resulted in a total loss of 0.89% of trials in the object condition, 1.04% in the belief condition and 0.93% of trials in the hand condition (0.95% over the whole experiment) on average. In addition the same error types (described in experiment 1a) could be incurred in this experiment. One participant's data was removed from analysis due to the fact that the participant did not comply with the pre-specified response instructions in the belief condition, and responded incorrectly.

Table 26: Mean % Anticipation errors, No-go errors and second response errors calculated as a percentage of the total number of trials where the error could occur for each type of error overall across the experiment. **Bold type** represents compatible trials.

Type of Error (total number of trials where error could occur)	Object Mean % Error	Belief Mean % Error	Hand Mean % Error	Overall Mean % Error
Anticipation Error (502)	0.20 (± 0.05)	0.59 (± 0.11)	1.11 (± 0.22)	0.63 (±0.05)
No-go Error (72)	4.28 (± 0.70)	4.53 (± 0.68)	5.92 (± 0.79)	4.91 (± 0.03)
Second response error (502)	0.00 (± 0.00)	0.01(± 0.01)	0.02 (± 0.02)	0.36 (± 0.00)

Table 27: Mean no-go and anticipation errors (± SE) for each stimulus. No-go errors were made out of a potential 72 and anticipation errors were made out of a potential 502. **Bold** type represents compatible trials.

Stimulus	Mean No-go errors (±SE)	Mean Anticipation errors (± SE)
Object	**1.24 (± 0.33)** 1.61 (± 0.35)	**0.12 (± 0.04)** 0.08 (± 0.03)
Object (belief)	**2.34 (± 0.45)** 2.19 (± 0.36)	**0.24 (± 0.08)** 0.35 (± 0.07)
Hand	**3.22 (± 0.54)** 2.70 (± 0.50)	**0.62 (± 0.13)** 0.49 (± 0.10)

4.2.2.2 Analysis of reaction time data

Overall mean RT (ms) (±SE) are presented in **Table 28**. Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects.

Table 28: Mean RTs (ms) (±SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (*p* < .05).

Stimulus/condition		SOA (ms)	Mean RT (ms) ± SE
Object	Press	0	**333.60 (± 8.79)** 340.55 (± 9.90)
		120	**310.48 (± 9.17)** 312.18 (±13.53)
		280	**299.32 (± 6.56)** 302.35 (± 6.86)
	Release	0	**336.44 (± 9.38)** 335.73 (± 8.90)
		120	**318.49 (± 8.70)** 319.01 (± 9.22)
		280	**304.10 (± 5.72)** 295.62 (± 7.67)
Object (belief)	Press	0	**350.47 (± 10.32)** 338.43 (± 8.71)
		120	**305.83 (± 9.39)** 299.06 (± 8.31)
		280	**270.44 (± 8.83)** 305.49 (± 8.30)*
	Release	0	**348.83 (± 11.29)** 345.15 (± 9.57)
		120	**313.58 (± 9.18)** 303.79 (± 7.47)
		280	**300.56 (± 5.65)** 289.58 (± 10.02)
Hand	Press	0	**335.12 (± 11.53)** 341.96 (± 14.95)
		120	**292.29 (± 9.90)** 308.52 (± 12.89)*
		280	**285.63 (± 11.42)** 319.80 (± 9.10)*
	Release	0	**339.79 (± 11.58)** 339.64 (± 14.31)
		120	**291.22 (± 7.58)** 298.26 (± 11.15)
		280	**314.21 (± 7.91)** 296.24 (± 9.36)

A mixed design (2x3x2x3) repeated measures ANOVA was conducted on participants' mean RTs with response type (press/release) x SOA (10, 120, 280) compatibility (compatible/incompatible) x condition (object/object with belief/hand) as within-subjects factors. There was a significant interaction between response and compatibility (*F*(1,18)= 7.586, *p* = .013); therefore pressing and releasing responses were analysed separately. Two separate repeated measures ANOVAs were conducted for pressing and releasing responses with SOA, compatibility, and condition as within-subjects factors. The usual main effect of SOA was present for both ANOVAs.

For pressing responses, there was a significant interaction between condition and compatibility (F(2,36) = 4.608, p = .017), a significant interaction between compatibility and SOA (F(2,36) =4.384, p = .020) and a significant three-way interaction between condition, compatibility and SOA (F(4,72) = 4.647, p = .002), indicating: 1) compatibility effects were significantly stronger for the object condition (M = 6.93ms) compared to the belief condition (-12.04ms) at 0ms (t(18) = 2.139, p = .046), however compatibility effects were significantly stronger for the belief condition (M = 35.05ms) compared to the object condition (M = 3.03ms) at 280ms (t(18) = -3.490, p = .003); 2) compatibility effects were significantly stronger for the finger condition (M = 6.84ms) compared to the belief condition (M = -12.04ms) at 0ms (t(18) = -2.408, p = .027), and significantly stronger for the finger (M = 16.23ms) compared to the belief condition (M = - 6.77ms) at 120ms (*t*(18) = -2.259, *p* = .037, however there was no significant difference at 280ms) (*t*(18) = .88, *p* = .931); 3) compatibility effects were significantly stronger for the finger condition (M=34.18ms) compared to the object condition (M=3.03ms) at 280ms (*t*(18) = -3.334, *p* = .004). **(Figure 58a)**. Significant main effects and interactions not directly relevant to the experimental hypotheses are presented in **Appendix B5**.

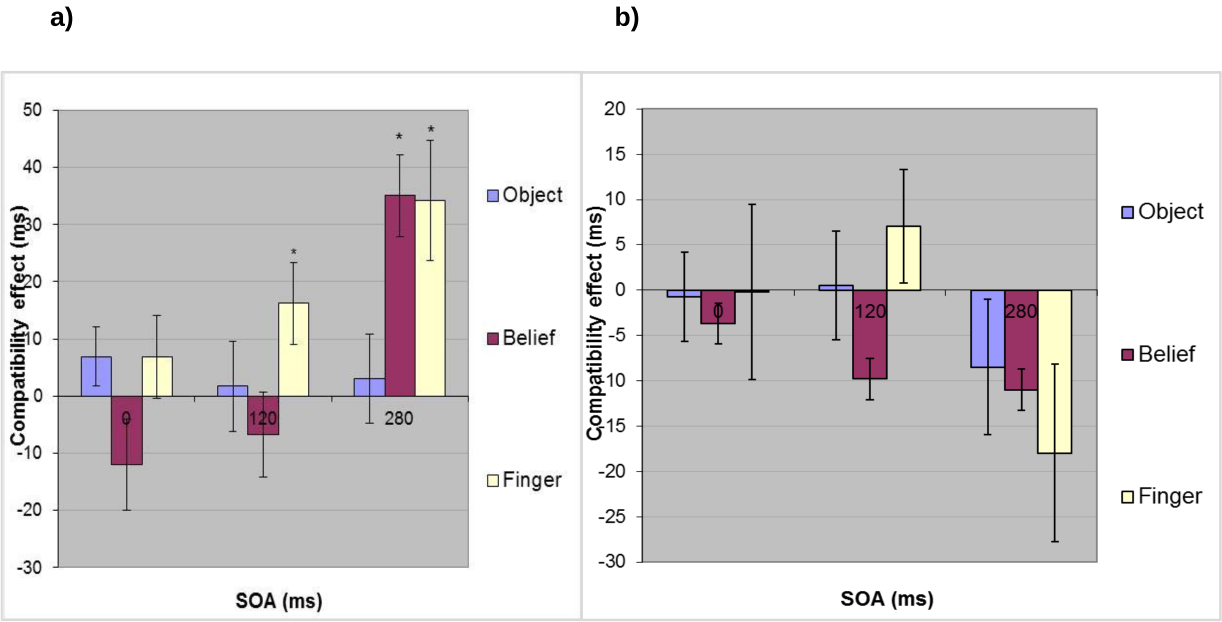


Figure 58: a) mean compatibility effects for each condition at each SOA for pressing responses; **b)** mean compatibility effects for each condition at each SOA for releasing response. Asterisks indicate significant compatibility effects

For releasing responses, no significant main effects or interactions relevant to the hypotheses were present **(Figure 58b)**. Significant main effects and interactions not directly relevant to the experimental hypotheses are presented in **Appendix B6**.

4.2.2.3 Analysis of questionnaire data

Mean questionnaire scores for belief questionnaire are presented in **Table 29**.

Table 29: Mean questionnaire scores for belief questionnaire in experiments 8 and 9. Questions 1.1-1.3 are from the initial questionnaire, completed following the object condition; Questions 2.1-2.6 were from the second questionnaire completed following the belief condition. In response to statement 1-6: a score of 10 represents 'agree'; 5 represents 'neither agree nor disagree' and 0 represents disagree. In response to questions 7-10: a score of 10 represents 'very much'; a score of 5 represents 'to some extent' and a score of 0 represents 'not at all'

Q. No	Question	Expt 8	Expt 9
1.1	During the first half of the experiment, did you at any time think that the moving rectangle might represent a human finger movement?	0.69	0.12
1.2	To what extent, if at all did the movement of the rectangle remind you of a human finger movement?	1.08	0.43
1.3	Seeing the rectangle move made me want to move my own finger	2.13	1.18
2.1	When you saw the rectangle for the second time, did you think of the rectangle as more of a 'block representation' of a moving finger, compared to when you had seen the rectangle for the first time?	6.45	7.59
2.2	When you saw the rectangle for the second time, to what extent did you think of the moving rectangle as being a human finger compared to when you had seen the block for the first time?	6.63	6.99
2.3	To what extent do you think that knowing that it represented a moving finger of a human hand influenced your perception of the movement, making the rectangle seem to move in a more human way, compared to when you saw the object the first time?	5.62	5.08
2.4	Seeing the rectangle move, in the knowledge that the movement represented a human finger movement, made me want to move my own finger.	4.45	3.96
2.5	When you were told the rectangle represented a finger movement, how much did you *believe* that this was true?	6.45	7.43
2.6	When you were told the rectangle represented a finger movement, how much did you *think about* this during the second half of the experiment?	6.55	7.59

With regard to the initial questionnaire which was designed to measure whether participants initially thought of the object as representing a human hand, participants reported that they did not think of or associate the object with a hand, in the object condition (prior to the belief manipulation). This is reflected in the RT data, as no imitative compatibility is present in the object condition.

Participants agreed to some extent that they did think of the object as representing a hand movement/being hand-like compared to the first time they saw the object in the belief condition; participants' mean scores for the four questions (Q2.1, Q2.2, Q2.3, Q2.5) pertaining directly to belief were between 5.62-6.63 (a score of 5 represents they believed 'to some extent' and a score of 10 represents they believed 'very much'). The response to Questions 2.5 and 2.6 indicated that participants reported that they were affected to some extent by the belief manipulation,

Each participant's 'belief' effect was calculated by subtracting each participant's maximum compatibility effects in the belief condition compared to maximum compatibility effects in the object condition. Questionnaire scores were collapsed across questions 2.1-2.5 to generate an average belief score.

We were interested in examining if there was any relationship between a) participants belief effect and empathy/AQ scores; b) participant's belief effect and self-reported average belief; c) self-reported average belief and EQ/AQ scores. However, we found no significant relationship between EQ (*r*(19)= .323, *p* = .177), or AQ (r(19)= -.337; p = .159) scores and 'belief' imitation scores in this experiment.

Pearson's correlations tests between belief effects and self-reported belief revealed a significant positive correlation between the belief imitation effect and their self-reported belief scores (*r*(19) = .677, *p* = .001) **(Figure 59)**.

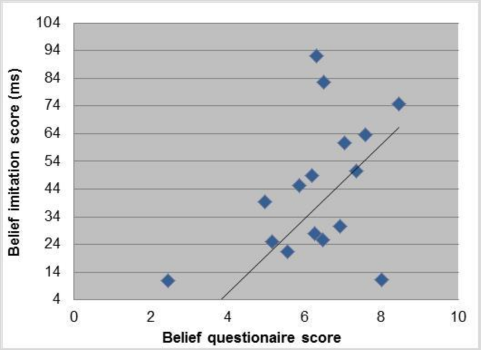


Figure 59: Positive correlation between participant's belief score and self-reported belief questionnaire scores

Pearson's correlations tests were carried out between EQ and AQ questionnaire scores an average score for self-reported effects of the belief manipulation. However, we found no significant relationship between empathy (*r*(19)= -.029, *p* =.906), or AQ (*r*(19)= .121, *p* = .621) and self-reported belief in this experiment.

4.2.3 Discussion

4.2.3.1 Potential belief effect contaminated with Simon effect

On initial inspection, it appears that the belief manipulation has worked as expected, as a large significant compatibility effect is present for the belief condition and for the finger is which is not present during the object condition. However, on closer inspection of the results, the pattern of compatibility effects is highly consistent with experiment 7. In both experiments the largest compatibility effects are observed at the final SOA in the pressing condition, and there are fewer significant effects for the releasing condition, for which reverse compatibility effects are present in the opposite direction at the final 280ms SOA. One likely explanation for this pattern of results (i.e. the unusually large compatibility effect observed in experiments 7 and 8 at the final SOA) (as discussed in **section 4.1.4.1**) is that, is that the compatibility effect is contaminated with a motion based Simon effect, which has become more apparent now that the smaller flash has focused attention more closely on the movement of the stimuli, and the stimuli have been rotated.

Simon effects or SRC effects on RTs are well documented for static situations. Importantly in relation to the current study, the Simon effect has been observed not only for stationary stimuli but for moving stimuli as well. For example in Michaels (1988) study, participants saw a rectangle that appeared to move towards or away from them, and participants responded by pushing a joystick towards the destination of apparent movement. They found that responses were faster when the stimulus appeared to move towards the responding hand, even when the stimulus location did not spatially correspond to the response location, indicating a Simon effect for a moving stimulus.

A widely held view is that a spatial code for stimulus location is formed even though it is not relevant to the task. A number of researchers have attempted to establish when and how this spatial code for irrelevant locations is formed, and two possible explanations have gained the most support (Lu and Proctor, 1995). Firstly, some researchers have argued that the ‘referential-coding account’ could be sufficient to explain the Simon effect (Hommel, 1993b). This account proposes that spatial stimulus coding depends on the availability of frames of reference i.e. the Simon effect results from a code generated when an object moves from one position to another because the original point of fixation (e.g. a fixation cross or object in the centre of the screen) acts as a reference object relative to the new location of the object. Indeed, in a number of studies on dynamic SRC the starting position of the stimulus was shown for some time before movement took place, supporting the idea that relative position coding may take place. In other words it has been suggested that the long exposure duration may have turned the starting point into a reference point, suggesting the current position of the target relative to the starting point is what is crucial in the appearance of a motion based Simon effect. In line with this theory, in a study in which a small light dot appeared and immediately moved no Simon effect was present.

However, this interpretation does not account for the fact that a study has found that no Simon effect occurred when attention remained at fixation during stimulus presentation, indicating the Simon effect is dependent on the direction of the attention movement toward the stimulus (Nicoletti and Umiltà, 1994). Therefore, an alternative ‘attentional-shift’ account has been proposed which posits that the stimulus spatial code is generated when there is a lateral shift of attention from the prior location to the target (destination) location, activating the saccade program which forms the spatial code of the stimulus, which in turn causes the Simon effect (Umiltà and Nicoletti, 1992; Nicoletti and Umiltà, 1994). Several points raised in the literature support the idea that a Simon effect for movement destination may have contaminated the results at 280ms in experiments 7-8. For example, the fact that the stimuli in experiment 7 and 8 are initially displayed in a neutral position for 1000ms prior to movement onset would give ample time for the initial position of the stimulus to act as a reference relative to the direction of movement, supporting the referential-coding account. As this theory suggests the Simon effect is a code generated when a stimulus moves from a starting point to a new location, it would make sense that the effect would emerge at 280ms (which is the 'destination' of the movement).

Alternatively, the attention orienting account posits that the Simon effect is based on orienting attention to the destination of the movement. As the intended 'destination' of the movement would become more apparent to the observer later in the movement this would potentially explain why the Simon effect is most apparent at 280ms as opposed to the earlier time points. Furthermore, it has been reported that the Simon effect is a transient effect which typically reduces with increasing response times (Rubichi et al., 1997). RTs were overall fastest at 280ms compared to the earlier SOAs. In addition, in order to explain the fact the Simon effect has been shown to be absent in studies if the relevant task is easy (e.g. discriminating between two different colours), Hommel (1993a) put forward the 'temporal overlap' theory, which suggests the absence of the Simon effect could be due to a lack of temporal overlap between relevant and irrelevant stimulus processing i.e. when the relevant task is easy it allows for fast processing of the relevant task therefore the irrelevant information (i.e. the spatial codes for stimulus location) has no time to take effect. Since imitative compatibility effects have been shown to increase with increasing RTs (Catmur and Heyes, 2011) it is likely that there is a larger temporal overlap between processing of the imitatively compatible movement and processing of the Simon effect at later SOAs compared to the earlier SOAs. Therefore, if the temporal overlap theory is correct, this could also explain why there was such a large effect at 280ms (i.e. the effect of imitative compatibility combined with the Simon effect brought out by the temporal overlap), as there may be less temporal overlap between the 'relevant' (imitative) and 'irrelevant' (Simon effect) processing at the earlier SOAs.

A Simon effect has not previously been evident in experiments 1-6, which suggests that the one of the changes made to the paradigm has brought out the effect. In experiments 7 and 8 we used a smaller focused flash go signal, and the object consisted of a single blue moving rectangle. It is therefore possible that the focused rectangular go signal was responsible for bringing out this effect, perhaps by drawing increased attention to leftward and rightward movement of the stimulus. This supports the idea that as suggested, less attention was focused on the area of stimulus movement when the diffuse flash was used as a go signal (hence the lack of a noticeable Simon effect in previous experiments). Since the location of the attentional focus when the stimulus is presented and attentional shift (Nicoletti & Umiltà, 1994; Rubichi et al., 1997) have both been shown to be important in the emergence of the Simon effect, this could explain why the effect has emerged only now that attention has been drawn to the stimulus movement. In addition, the fact the object stimulus consisted of a single moving object could also have produced increased attention to the object movement.

However, encouragingly, for the pressing response, while the compatibility effect was particularly large for the belief and hand conditions, no compatibility effect was present for the object condition prior to the belief manipulation. This can be attributed to the fact that in this condition, the compatibility effect would be caused by both the Simon effect and imitative compatibility. The fact that this effect is not present in the object condition suggests two non-mutually exclusive possibilities: a) participants are paying less attention to the direction of stimulus movement in the object condition; b) imitative compatibility is not present in this condition as it is prior to the belief manipulation, however orthogonal compatibility was present (Right/up, Left/down), and is in competition with the Simon effect, leading to a null effect overall in this condition. Therefore, the Simon effect could also potentially explain why there is a lack of clear orthogonal compatibility effects for the object stimulus present in experiments 7 and 8. Furthermore, it suggests that belief may have affected level of imitation; however it will be important to isolate imitative compatibility from both orthogonal spatial compatibility and the Simon effect to draw any firm conclusions regarding the origin of the effect of belief.

4.2.3.2 Questionnaire data findings

The questionnaire data suggests that there is no relationship between empathy/AQ and belief imitation scores, or self-reported belief scores. There was, however, a significant positive correlation between the effect of belief on imitative compatibility and self-reported belief scores. This suggests that there is a relationship between the amount that a person consciously believes that the non-biological stimulus represents a human stimulus and their subsequent imitation of the object as if it were human. This suggests that the belief effect may be an explicit rather than an implicit effect in cases where the instruction if given verbally. It suggests that participants who did not believe the manipulation did not show the same modulation of imitation, as they did not believe it to be human generated. However, importantly, since we are measuring imitation that is contaminated with the Simon effect, this may not be an accurate representation of these relationships.

4.2.4 Conclusion

In this penultimate experiment, we have established that the pattern of compatibility effects (where a large positive compatibility effect was present at 280ms for pressing, and a large negative compatibility effect at 280ms was present for releasing) is consistent with an additional influence of a Simon effect contaminating the imitative compatibility effects in experiments 7 and 8. Encouragingly, however, the results of experiment 8 do suggest that an effect of belief was potentially present, as no imitative compatibility effects were present for the object stimulus until the ‘human’ belief was introduced. However, in order to draw any firm conclusions regarding the cause of the belief effect, it will be important to fully isolate the imitative component from both orthogonal spatial compatibility and the Simon effect. This is addressed in experiment 9.

4.3 Experiment 9 - Introduction

In experiment 9, we aimed to design an experiment in which imitative compatibility effects could be fully dissociated from both orthogonal compatibility effects *and* the Simon effect. We therefore altered the paradigm in order to remove the Simon effect and isolate the imitative component of the compatibility effect. In the improved version of the paradigm we presented a right-handed stimulus rotated clockwise, and participants were required to use their left hand to respond by pressing a key (releasing response was not used in this experiment). Participants were presented with a right hand stimulus (mirror image of the participants left hand) rotated 90 degrees counter clockwise, in a 'thumb up orientation' (see **Figure 60**). This method would effectively separate the Simon effect (left advantage due to using left hand to respond) and orthogonal spatial compatibility effects (down-left advantage when pressing button) from imitative compatibility (finger moving down i.e. right movement would be imitatively compatible). This is because, in terms of imitative compatibility, in this orientation, when the observed finger stimulus is moving downwards (rightwards movement direction) this would be imitatively compatible with the participant's press response, and when the finger is moving upwards (left movement direction) this would be imitatively incompatible with a press (down) response. However, both orthogonal spatial compatibility and the Simon effect are compatible for the opposite movement direction to the imitative compatibility effect i.e. observing the finger lifting (leftward movement) would be compatible and observing the finger moving downwards (rightward movement) would be incompatible with the participant's response **(Figure 61a).**

We used an identical overall structure to that of experiment 8 to explore the belief effect using this improved task. We hypothesized that in an ideal situation, in the thumb up orientation. We hypothesized that in an ideal situation, in the thumb up orientation, we would get a dissociation between imitative compatibility effects (shown by a positive compatibility effect) and orthogonal spatial compatibility/Simon effect (shown by a negative compatibility effect. We would expect orthogonal spatial compatibility/Simon effect to be present in the initial object condition (but no imitative compatibility should be present as the object is initially associated with a left/right movement). In the belief condition we hypothesized that: 1) there would be an increase in orthogonal spatial compatibility/Simon effect if the belief effect represented increased attention following the belief manipulation; or 2) there would be an imitative compatibility effect present for the object in the belief condition if the belief effect represented a 'true belief' effect. We would expect imitative compatibility to be present for the hand stimulus, which may be similar to the belief condition if the belief effect represents true belief.

However, a potential disadvantage of this experiment is that we would be playing both Simon and orthogonal spatial compatibility effects against imitative compatibility effects which could potentially significantly weaken imitative compatibility effects. In addition, the imitative compatibility effect may also be weaker and more variable because right-handed participants would be using their left hand rather than their dominant hand to respond. Based on this, we expected that the imitative compatibility effects produced might be relatively small. Therefore, we included a ‘thumb down orientation’ as a control situation (see **Figure 61b**), as this orientation combines imitative compatibility, orthogonal spatial and the Simon effect, as all three are compatible with the finger moving downwards (left movement direction) and a left-handed pressing response; and all three are incompatible with the finger moving upwards (right movement direction) and a left-handed pressing response. We would therefore expect a large positive compatibility effect representing all types of compatibility effect combined. This would enable us able to subtract orthogonal spatial compatibility/Simon effect in the thumbs up orientation from the effect for all three combined in the thumbs down control orientation, theoretically allowing us to indirectly calculate the size of the imitative compatibility effect.

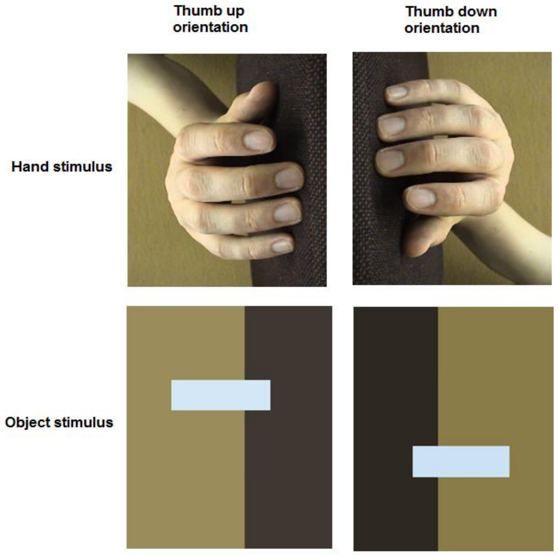
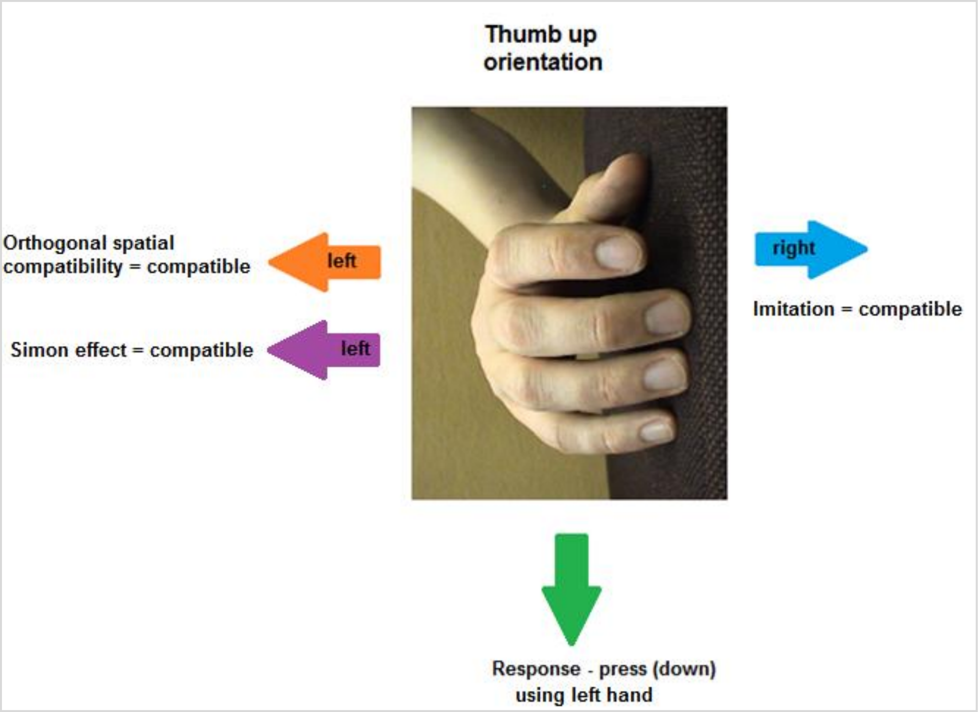


Figure 60: Thumb up and thumb down orientation images of the hand and object stimuli.

a)



b)

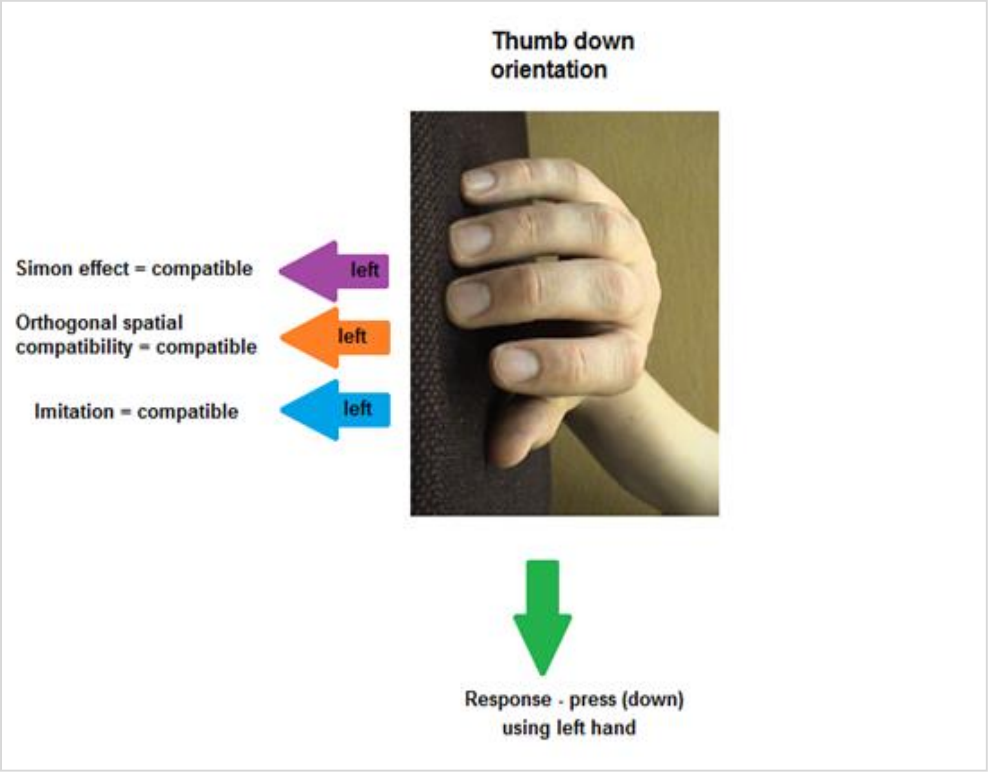


Figure 61: a) In the thumb up orientation, imitative compatibility is pitted against orthogonal spatial compatibility and the Simon effect; **b)** In the thumb down direction the Simon effect, orthogonal spatial compatibility and imitation are all compatible in the same direction.

4.3.1 Methods

4.3.1.1 Participants

20 right-handed healthy individuals were recruited for the study; however, two participants' data was excluded from analysis due one participant to not complying with the instructions and therefore not changing response in one of the blocks, and one participant producing 'anticipation errors' on all 280ms responses in the hand condition. The mean age (±SD) of the remaining 18 participants (10 female) was 22.94 (± 4.71). The mean laterality quotient was 96.89 (±7.61). The study consisted of a single testing session lasting approximately 90 minutes, and participants were paid £7.50 for their participation.

4.3.1.2 Design and procedure

A rotated right hand stimulus was presented and participants were required to respond with their left hand. The participant's response was to press the button throughout the experiment (no release response).

The experiment consisted of a total of 576 trials. The experiment was split into three sections. In the object condition, the object stimulus was presented. Prior to the belief condition, where the object was presented again (in thumb up and thumb down orientation) participants were told that the object stimulus movement was generated from a human finger movement. Participants were shown a printed picture of the hand and it was made clear the orientation of the hand for the thumb up/thumb down orientations. Finally, in the finger, participants observed the hand stimulus. A short break was given every 48 trials (one block). There were 4 blocks of 48 trials in each of the three sections of the experiment. Two of the four blocks presented the stimulus in a 'thumb up' orientation (48 x 2 = 96 trials) and the other two blocks presented the stimulus in a 'thumb down' orientation (48 x 2 = 96 trials). The starting orientation (thumb up/thumb down) was counterbalanced across participant. The starting orientation was the same for each of the three sections of the experiment. A longer break was given every 192 trials (48 x 4) (after each section).

As in previous experiments participants completed the empathy questionnaire, AQ questionnaire, ELI questionnaire. As in experiment 8, participants completed the first part of the belief questionnaire after Section 1 (object stimulus), and the second part of the belief questionnaire on completion of the experiment.

4.3.2 Results

4.3.2.1 Analysis of error data

The same exclusion criterion used in previous experiments was applied. This resulted in a total loss of 0.39% of trials on average in the thumb up orientation and 0.45% on average in the thumb down orientation. Mean percentage errors are presented in **Table 30 and Table 31**. In addition, the same error types (described in experiment 1a) could be incurred in this experiment.

Table 30: Mean % Anticipation errors, No-go errors and second response errors calculated as a percentage of the total number of trials where the error could occur for each type of error overall across the experiment. **Bold type** represents compatible trials

Type of Error	Thumb up Object Mean error (± SE)	Thumb up Belief Mean error (± SE)	Thumb up Hand Mean error (± SE)	Thumb down Object Mean error (± SE)	Thumb down Belief Mean error (± SE)	Thumb down - Hand Mean error (± SE)
Anticipation Error (502)	0.02 (± 0.01)	0.10 (± 0.06)	0.16 (± 0.05)	0.10 (± 0.04)	0.14 (± 0.06)	0.12 (± 0.02)
No-go Error (72)	0.88 (± 0.00)	2.05 (± 0.37)	1.83 (± 0.41)	1.10 (± 0.27)	1.46 (± 0.38)	1.46 (± 0.47)
Second response error (502)	0.01 (± 0.01)	0.01 (± 0.01)	0.03 (± 0.02)	0.06 (± 0.03)	0.01 (± 0.01)	0.01 (± 0.01)

Table 31: Mean no-go and anticipation errors (± SE) for each stimulus. No-go errors were made out of a potential 72 and anticipation errors were made out of a potential 502. **Bold** type represents compatible trials.

Stimulus	Mean No-go errors (± SE)	Mean Anticipation errors (± SE)
Thumb up - Object	**0.29 (± 0.17)** 0.58 (± 0.19)	**0.00 (± 0.00)** 0.02 (± 0.01)
Thumb up – Belief	**0.00 (± 0.19)** 1.32 (± 0.25)	**0.06 (± 0.04)** 0.04 (± 0.02)
Thumb up – Hand	**1.02 (± 0.28)** 0.80 (± 0.27)	**0.08 (± 0.03)** 0.07 (± 0.03)
Thumb down – Object	**0.22 (± 0.16)** 0.88 (± 0.24)	**0.05 (± 0.02)** 0.05 (± 0.03)
Thumb down – Belief	**1.02 (± 0.30)** 0.44 (± 0.15)	**0.07 (± 0.03)** 0.06 (± 0.03)
Thumb down -Hand	**1.02 (± 0.26)** 0.44 (± 0.24)	**0.05 (± 0.02)** 0.06 (± 0.02)

4.3.2.2 Analysis of reaction time data

Overall mean RTs (ms) (±SE) are presented in **Table 32**. Paired t-tests were carried out between compatible and incompatible RTs for each experimental condition to show the presence or absence of significant compatibility effects.

Table 32: Mean RTs (ms) (±SE) of participant's responses for each condition. **Bold** type indicates a compatible response. Asterisks indicate statistical significance of paired t-tests for compatible and incompatible responses (*p* < .05).

Condition	SOA	Mean RT (ms) (± SE)	
		Thumb up orientation	Thumb down orientation
Object	0ms	**355.03 (± 9.64)** 349.78 (± 9.89)	**346.2488 (± 10.51)** 351.9550 (± 11.57)
	120ms	**331.19 (± 10.91)** 317.77 (± 9.06)*	**323.8137 (± 12.02)** 315.2426 (± 12.03)
	280ms	**322.98 (± 7.34)** 311.58 (± 9.16)	**315.2426 (± 11.64)** 313.7001 (± 11.37)
Belief	0ms	**389.64 (± 17.38)** 390.63 (± 21.03)	**386.0974 (± 16.22)** 385.6174 (± 14.43)
	120ms	**334.33 (± 15.44)** 346.63 (± 19.41) **p =.052*	**340.6232 (± 15.43)** 337.5374 (± 15.38)
	280ms	**332.21 (±12.84)** 337.53 (±16.11)	**331.7474 (± 10.14)** 330.1622 (± 13.27)
Hand	0ms	**378.24 (± 16.38)** 373.76 (± 13.44)	**366.8028 (± 10.37)** 367.7733 (± 12.99)
	120ms	**319.93 (± 9.81)** 327.53 (± 14.59)	**322.3665 (± 12.10)** 323.8160 (± 12.01)
	280ms	**316.01 (± 11.19)** 325.16 (± 11.21)	**318.4494 (± 11.23)** 322.7461 (± 11.85)

RTs for stimuli presented in thumb up/thumb down orientations were analysed separately, as we had separate hypotheses for each orientation. A repeated-measures ANOVA was conducted for the Thumb down orientation with condition (object/belief/hand), SOA and compatibility as within-subject factors. No significant main effects or interactions relevant to the hypotheses were present **(Figure 62)**. Significant main effects and interactions not directly relevant to the experimental hypotheses are presented in **Appendix B6**.

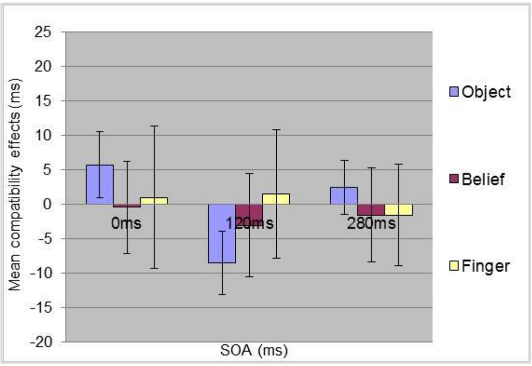


Figure 62: Mean compatibility effects (± SE) in thumb down orientation over all 3 conditions (Object, Belief, Hand) across 3 SOAs. Error bars indicate the standard error of the mean.

A repeated-measures ANOVA for the Thumb up orientation with condition (object/belief/hand), SOA and compatibility as within subjects factors was conducted on mean RTs.

There was a significant interaction between condition and compatibility (*F*(2,34) = 5.461, *p* = .009). Paired t-tests were conducted between mean compatibility effects in each condition (averaged across SOA) indicating that mean compatibility effects were significantly weaker for the object (going a negative direction and therefore representing orthogonal spatial compatibility/Simon effect) (mean = -10.04) than both the belief condition (mean = 6.20) (*t*(17)= -3.024, *p* = .008) and the hand conditions (mean = 4.09)) (*t*(17)= -2.535, *p* = .021) (both going in a positive direction and therefore representing imitative compatibility effects **(Figure 63 and Figure 64);** while there was no significant difference between the positive (imitative) compatibility effects between the belief and hand conditions (*t*(17)= .416, *p* = .628). In fact, a Pearson's correlation test between the compatibility effects for the hand (mean compatibility effect = 3.83ms) and belief condition (mean compatibility effect = 3.55ms) showed a significant positive correlation (*r*(18)= .491, *p* = .039) **(Figure 65)**.

The interaction between compatibility, condition and SOA did not reach significance (*F*(4,68)= 1.018, *p* = .404). However, paired t-tests showed a significant negative compatibility effect (representing orthogonal spatial compatibility/Simon effect) was present at 120ms for the object condition (*t*(17) = 2.625, *p* =.018), and the positive compatibility effect (representing imitative compatibility) at 120ms in the belief condition was approaching significance (*t*(17) = -2.089, *p* =.052). The compatibility effects for the finger did not reach significance at any of the SOAs (*p* > .307); however they followed the same pattern as the belief condition with positive compatibility effects (representing imitative compatibility) present at 120ms and 280ms. Significant main effects and interactions not directly relevant to the experimental hypotheses are presented in **Appendix B6**.

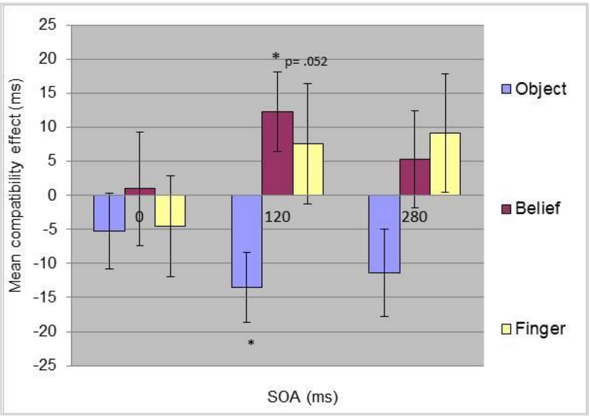


Figure 63: Mean compatibility effects (± SE) in thumb up orientation over all 3 conditions (Object, Belief, Hand) across 3 SOAs

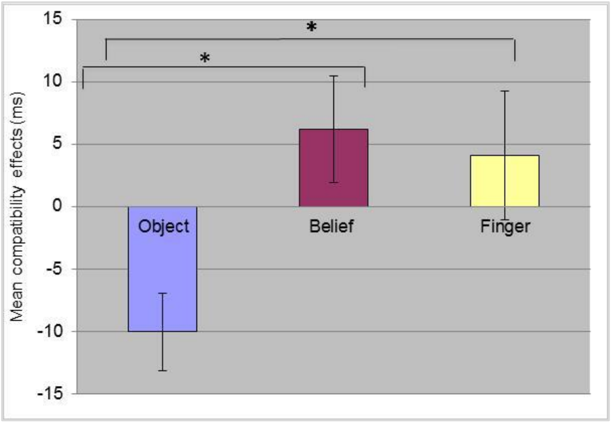


Figure 64: Mean compatibility effects (± SE) for the finger, object and belief conditions (averaged across SOAs)**.** There was a significant difference between compatibility effects for the object and belief condition. There was also a significant difference between compatibility effects for the object and finger condition

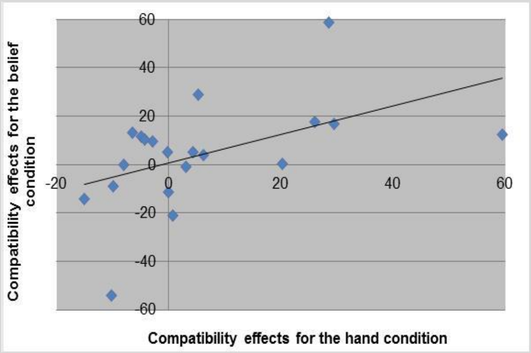


Figure 65: Positive compatibility effect between compatibility effects for the hand condition and compatibility effects for the belief condition

4.3.2.2 Analysis of questionnaire data

As in experiment 8, participants completed a 'belief' questionnaire as a self-reported measure of the extent to which the belief manipulation altered their view of the object stimulus to make it seem more biological, and to what extent the belief manipulation was successful. Mean questionnaire scores are presented in **Table 31 (Section 4.2.2.3)**

Again, participant's responses to questions 1.1 and 1.2 show that participants reported that they did not think of or associate the object with a hand, in the object condition (prior to the belief manipulation) (mean score = 0.12-0.43). This reflects the RT data since orthogonal spatial compatibility/Simon effect compatibility is present for the object (and no initial imitation is present).

Participants indicated that they did think of the object as representing a hand movement/being hand-like to some extent in the belief condition; participant's mean scores for the four questions (Q2.1, Q2.2, Q2.3, Q2.5) pertaining directly to belief were between 3.86-7.59 (a score of 5 represents they believed 'to some extent' and a score of 10 represents they believed 'very much'). The response to Question 2.5 indicates that participants reported that they were affected to some extent by the belief manipulation, as the mean score for the question ‘When you were told the block represented a hand movement, how much did you *believe* that this was true?’ was 7.43, and the mean score for how much they thought about this during the belief condition section of the experiment was 7.54.

We were interested in examining if there was any relationship between a) participants belief effect and EQ/AQ scores; b) participant’s belief effect and self-reported belief; and c) self-reported belief and EQ/AQ, in the thumb up orientation only due to the fact it followed the expected pattern. Each participant’s ‘belief effect’ was calculated by subtracting each participant’s minimum compatibility effect in the object condition (in which we expected negative compatibility effects) from their maximum compatibility effects in the belief condition (in which we expected positive compatibility effects). Questionnaire scores were collapsed across questions 2.1, 2.2, 2.3 and 2.5 to generate an average belief questionnaire score.

There was no significant correlation between each participants belief effect and empathy (*r(18)* = .168, *p* =.506) or AQ (*r* = .246, *p* =.325). There was no correlation between the belief effect and self-reported belief (*r*(18) = .342, *p* =.165). Finally, there was no significant correlation between self-reported belief scores and empathy (*r*(18) = .029, *p* = .910) or AQ scores (*r*(18)= .179, *p* =.478).

4.3.3 Discussion

This final experiment has produced three highly significant findings. Firstly, in the thumb down orientation, we have successfully isolated imitative compatibility effects from orthogonal spatial compatibility and the Simon effect, thus giving a pure measure of imitative compatibility effects. Secondly, we hypothesized that increased imitative compatibility effects in the belief condition would represent a ‘true belief’ effect, while increased orthogonal compatibility effects/Simon effect would constitute increased attention to the object stimulus in the belief condition. We found imitative compatibility effects were present in the belief condition, indicating that the effect of belief is based on a ‘true belief’ effect as opposed to increased attention in the belief condition. Finally, the results in the thumbs down condition did not follow our predictions of a stronger overall effect (due to combining imitative compatibility with orthogonal spatial compatibility and the Simon effect). In addition, we did not find any correlation between EQ/AQ and pure imitative compatibility effects. These results will now be discussed in further detail.

4.3.3.1 Thumb up orientation - isolation of imitative compatibility from spatial SRC effects

We have determined that the compatibility effect for the object condition is initially based purely on orthogonal spatial compatibility/the Simon effect, as participants’ responses were faster to stimuli moving to the left (down-left orthogonal advantage/left-hand response faster when stimuli moving to the left) and slower to stimuli moving to the right. However, imitative compatibility effects are present for the belief condition and the hand condition (where participants are instead reacting faster to stimuli moving to the rightward direction (depicting the finger moving downwards) as this is compatible with their pressing response. This pattern of results indicates we have successfully separated spatial and imitative compatibility effects, providing a pure measure of imitative compatibility effects, despite the fact we have played imitative compatibility against the spatial compatibility effects (where the leftward movement direction has the advantage). This suggests that the imitative compatibility effect is a stronger effect than these spatial compatibility effects for human movements and for movements believed to be human generated. The moving rectangle on the other hand was not initially associated with an upwards or downwards movement prior to belief being manipulated, and therefore the advantage was for the leftward direction due to orthogonal spatial compatibility and the Simon effect; and no imitative compatibility effects were observed.

Previous studies which have compared imitative compatibility effects for biological compared to non-biological stimuli have reported reduced or no imitation of non-biological stimuli (Kilner et al., 2003; Press et al., 2006) however it has been argued that it is difficult to know how much of the difference in response can be attributed to differences in stimulus saliency, or to fully control for these saliency differences (Boyer et al., 2012). In addition, some studies have revealed no difference in levels of activation when observing human and non-human movements (Jansson et al., 2007; Stanley and Miall, 2007) and on that basis it has been argued that imitative compatibility could simply represent a specialised form of SRC (Jansson et al., 2007).

Importantly, this improved version of the rotated paradigm has allowed us to separate imitative compatibility effects from spatial compatibility effects and the Simon effect. The fact that the methodology used in this experiment allowed us to successfully isolate the imitative component is a highly significant finding. The experiment shows that contrary to the suggestions of some researchers (Aicken et al., 2007; Jansson et al., 2007) imitative compatibility effects are not simply reducible to spatial compatibility effects.

The current findings therefore validate the use of ‘automatic imitation’ paradigms to measure imitative compatibility effects. However, these findings also confirm that in previous studies in which imitative compatibility and automatic imitation were confounded, the observed compatibility effect is likely to have resulted from a combination of spatial compatibility and imitative compatibility effects; and therefore may not have provided an accurate measure of pure imitative compatibility effects. It also suggests that previous studies which have previously found ‘imitative compatibility’ effects for object stimuli may have actually been due to confounding spatial compatibility effects (unless the participants - either implicitly or due to explicit instructions - associated the object movement with a human movement).

4.3.3.2 A top-down belief effect

There are two potential interpretations of the influence of belief regarding agency on imitative compatibility effects observed in previous studies. Firstly, manipulating belief regarding agency could cause increased interest in a non-biological stimulus in the human belief condition, thus increasing the amount of attention they pay to the stimulus and consequently increasing SRC effects. Secondly, human belief regarding agency may have a top-down influence over imitative compatibility effects by upregulating MNs associated with human finger movement. We have found the initial orthogonal spatial compatibility/Simon effect observed for the object in the object condition reversed completely in the belief condition, where an imitative compatibility effect was present for the object, despite the fact the object stimulus was perceptually identical in both conditions. The current results therefore support the true belief hypothesis. Had the ‘attention hypothesis’ been correct, and the belief manipulation caused increased attention to the object stimulus, then there would have been a further increase in orthogonal spatial compatibility effects and the Simon effect in the belief condition. However, the fact that imitative compatibility effects are present for the object following the belief manipulation suggests the information regarding agency modulated their behaviour, causing participants them to respond to the object stimulus movement as if it were a human generated finger movement.

It is interesting to note that overall RTs were slower for the hand compared to the object, despite the stimulus being the same. One explanation for this difference is that if participants believed the object to represent a human hand they may have mentally rotated the object stimulus (as if it were a hand). This supports the idea that participants imagined the movement of the rectangle as if it were a human finger movement. The idea that participants may have been mentally rotating the stimuli is discussed in further detail in **Section 4.3.3.3**.

Participant’s responses to questions 1.1 and 1.2 of the initial questionnaire show that participants reported that they did not think of or associate the object with a hand, in the object condition (prior to the belief manipulation), and this reflects the RT data since orthogonal spatial compatibility/Simon effect compatibility is present for the object (and no initial imitation is present). In addition, participants indicated that they did think of the object as representing a hand movement/being hand-like compared to the first time they saw the object in the belief condition to some extent; participant’s mean scores for the four questions (Q2.1, 2.2, Q2.3, Q2.5) pertaining directly to belief were between 5.34-7.66. No relationships were present between empathy and AQ scores, belief scores and self-reported belief questionnaire scores. It is possible that this is due to a lack of spread in participant’s empathy and AQ scores

4.3.3.3 Thumb down orientation - mental rotation difficulty

The thumb down orientation was included as a ‘control’ in the event that imitative compatibility effects were too weak in the thumb up orientation due to playing imitation against spatial compatibility and the Simon effect, and using the non-dominant left hand to respond. Unlike the results for the thumb up orientation, however, the results for the thumb down orientation results did not follow a clear pattern.

One explanation for this is that in order to imagine the movement as a human finger movement, the participants may have either mentally rotated the stimuli to match their own hand position, or mentally rotated their own hand in order to match the stimulus position. Since matching the stimuli to one's one hand position would be easier in order to process the stimulus movement as normal up/down movement in the hand/belief conditions, it seems more likely that participants may have mentally rotated the stimuli to match their own hand position.

For the thumb down orientation mentally rotating the stimulus to match the position of one's own left hand is a more biomechanically complicated movement than rotating the thumb up orientation to match one's own left hand position **(Figure 72)**, which could explain the results. The fact that participants responded faster overall in the object stimulus condition compared to the belief and the hand condition (see **Appendix**) validates this argument as the increased time could be accounted for by the extra time and resources needed to mentally rotate the stimulus, which is not needed in the initial object condition. This account makes sense given that in the thumb up orientation, imitative compatibility effects are present in the hand and belief conditions, but not in the object condition in which there would be no reason to mentally rotate the stimulus.

The first evidence for mental rotation came from Shepard and Metzler's (1971) seminal experiments in which participants were required to judge whether two rotated abstract block figures were the same or different. They found that there was a positive linear relationship whereby response times for the judgement increased with the increasing angle of rotation between the presented figures. This finding has been interpreted as indicating that people mentally rotate figures to match each other. With greater relevance to the current study, some later mental rotation studies have used a paradigm in which the participants were required to judge an object or body part laterality, referred to as a laterality judgment task.

The first study of this kind found that the RTs for judging hand laterality increased with increasing angle of rotation (Sekiyama, 1982). A number of other studies have corroborated the idea that participants solve hand laterality judgement tasks by imagining their own hand rotating until it matches with the presented stimulus orientation (Parsons, 1987; Ganis et al., 2000). Such hand laterality judgement studies have consistently found that the time required to judge hand laterality is equivalent to the amount of time taken to actually execute the movement (Parsons, 1987, 1994).

Evidence from several neuroimaging studies suggests a substantial cognitive and neural overlap between hand laterality judgement tasks and the actual execution of actions (Rumiati et al., 2001; Tomasino et al., 2003; De Lange et al., 2005; Parsons, 1994).

Importantly, in terms of interpreting the results of the current study, participant's performance during a mental rotation task of hands is known to be influenced by biomechanical constraints (Parsons, 1987, 1994). The imagined movement trajectory during hand laterality judgements was strongly influenced by the biomechanical constraints of real left/right hand movements, such that movements that are difficult to produce in real life (due to the fact the postures were incompatible with the way the human wrist and arm joints move) were also difficult to rotate mentally (thus causing slower handedness judgements) (Parsons, 1994). Specifically, Parsons and colleagues (1994) found difficult-to- adopt lateral hand rotations (away from the midline) resulted in slower RTs for judgements of laterality than easy-to-adopt postures (e.g. medial hand rotation (toward the midline) for both real and imagined movements.

It is possible that in our experiment participants are mentally rotating the stimulus to match one's own hand position in a similar way to in the hand laterality judgement task. Parsons et al. (1994) showed that it is bio-mechanically easier to mentally rotate a right hand clockwise (towards the midline). Mentally rotating the observed thumb up stimulus to match one's own left hand would involve a simple clockwise 90 degree rotation of the thumb up stimulus hand therefore the posture is biomechanically easy-to-adopt. Conversely, they also showed that it is bio-mechanically more difficult to rotate a right hand counter-clockwise (away from the midline); therefore mentally rotating the thumb down stimulus to match one's left hand would be more difficult as this would involve a 90 degree counter-clockwise movement **(Figure 66)**.

In addition, an fMRI study by De Lange et al. (2005) found that the position of the participants own left or right arm influenced the laterality judgements of left and right hands. Hand laterality judgements was observed to activate a parieto-frontal network and the activity within this network increased with increasing biomechanical complexity of the imagined hand movements, even when the amount of stimulus rotation was identical. Therefore, despite the fact both the thumb up and thumb down orientation stimuli are both rotated 90 degrees, the biomechanical complexity of mentally rotating the thumbs down orientation compared to the thumb up orientation could explain why we achieved the predicted pattern of the results for the thumb up orientation but not for the thumb down orientation.

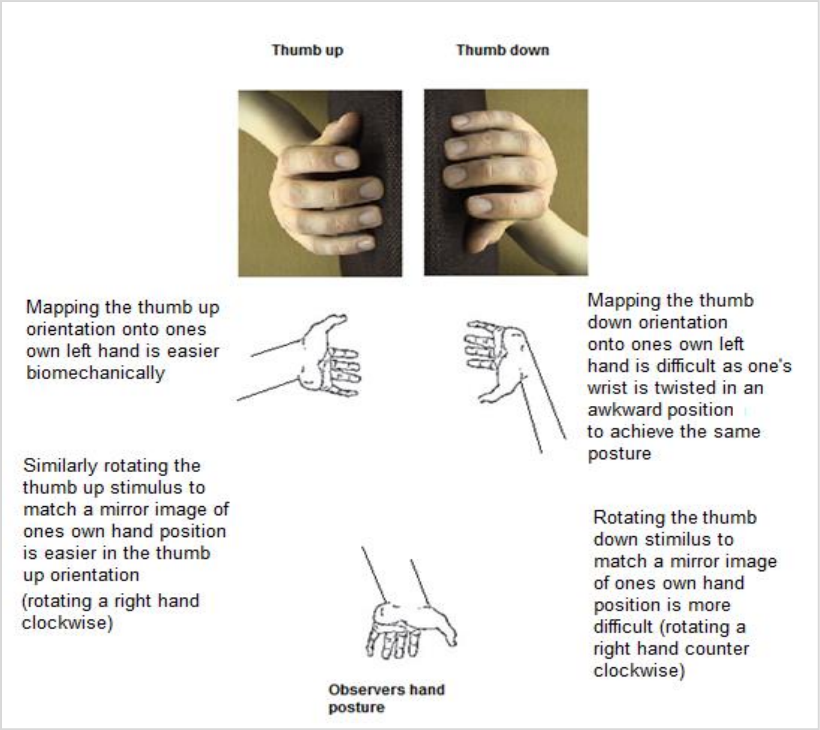


Figure 66: Rotating ones left hand into the thumbs up position would involve a natural movement, whereas rotating ones left hand into the thumbs down position would involve an unnatural movement.

4.3.3.4 EQ/AQ findings

No correlations were observed between empathy/ASQ and the pure measure of imitative compatibility. Some previous studies have found relationships between these variables, however, these studies have not fully controlled for spatial compatibility effects and so may not have been a true representation of the relationship. It is also possible that such a relationship might only apply to more emotional stimuli (e.g. emotional facial expressions), with which most previous correlations with empathy have been found. The lack of correlations might also be due to a lack of spread in participant’s empathy and AQ scores in the current study. In addition, as is widely known, self-report questionnaires can be influenced by a variety of interfering factors. For example, the score might not indicate how one actually felt but rather reflect what one believes one is expected to feel. Further reasons for these null findings will be discussed in **section 5.4**.

4.3.4 Conclusion

In this final experiment, we have successfully dissociated imitative compatibility from orthogonal spatial compatibility and the Simon effect. When participants viewed the stimuli in the thumb up orientation we found that initially orthogonal spatial compatibility/the Simon effect are present for the object stimulus. However, following the belief manipulation, imitative compatibility was present for the object stimulus. This indicates that the belief manipulation led participants to alter their behaviour and respond to the object movement as if it were a human finger movement. This suggests that the belief effect was not due to simply increasing their attention to the stimulus following the belief manipulation, as some researchers have argued. The results show that the way in which the participants responded to the object in the belief condition was very similar to the way they responded to the real hand in the final hand section of the experiment. However, the thumb down orientation has produced unexpectedly messy results, which is likely due to the fact the thumb down orientation would be more difficult to mentally rotate.

Chapter 5

General Discussion and Future Directions

5.1 Overview of main findings

The primary aim of this thesis was to provide further evidence that ‘automatic’ imitation is influenced by the top-down factors of attention and belief, in the absence of confounding factors such as spatial compatibility. In particular, the work presented in this thesis has clearly shown that the top-down factors of attention and belief have a strong modulating influence on the magnitude of imitative compatibility effects produced. This indicates that while ‘automatic’ imitation is automatic in the sense of being outside of one’s intentions and conscious awareness, it not a completely automatic process (i.e. it is not immune from interference from higher cognitive processes). In addition, the control of imitation appears to draw on general processing resources.

The following tables provide an overview of the key findings in each of the experiments in each chapter of this thesis **(Table 31, 32 and 33)**. The key themes which have emerged from this thesis are then discussed in further detail.

Table 31: Chapter 2 key findings and implications

Expt.	Key findings	Implications
1a	Reinstated human bias of imitative compatibility using a diffuse flash go signal presented at earlier SOAs.	Implied that imitative compatibility effects are sensitive to general attentional strategy (based on comparison with Gowen et al (2010)). In addition, suggests attention is required for differentiation between human and non-human stimuli.
1b	The secondary visual task which was included to draw attention to the movement of the stimulus, conversely removed the human bias.	The unexpected finding that even an easy secondary visual task removes imitative compatibility effects raised the question as to whether the removal of imitation was due to accessing the same sensory modality as imitative compatibility, or due to general cognitive load.
2	Using the auditory secondary task there were stronger imitative compatibility effects for the finger stimulus relative to experiment 1a. Compatibility effects for the object stimulus were also produced.	The removal of imitation in experiment 1b was due to the fact the visual secondary task was in the same sensory modality, thus was in competition for cognitive resources used for imitative compatibility. There results also indicated there may be a baseline level of inhibition of imitation (in experiment 1a).
3	When the finger and object stimuli were presented in separate blocks, a significant imitative compatibility effect for the object stimulus was present in the group of participants who observed the finger first.	Preliminary evidence for an implicit belief effect, such that participants associated the object movement with the previously observed finger movement.

Table 32: Chapter 3 key findings and implications

Expt.	**Key findings**	**Implications**
4	Automatic imitation effects produced, despite spatial compatibility being pitted against automatic imitation. Replicated the finding of imitative compatibility effects for the object stimulus in the 'finger first' group.	Supports the idea that previously observing the finger stimulus may have caused an implicit belief effect, whereby the human agency of the previously observed finger movement carried over to the object stimulus.
5	Unusually an imitative compatibility effect for the object was initially present. This initial effect reduced after the human hand stimulus was presented, and decreased further after a human belief regarding stimulus agency was instilled.	Observing a real biological hand stimulus may have led to the subsequent reduction in the initial imitation for the object, as it may have appeared less biological following observation of the real human hand, potentially altering participants' initial implicit beliefs.
6	No imitative compatibility effects were initially observed for the object prior to belief. Furthermore, a non-significant trend for imitative compatibility for the object stimulus was observed in the belief condition.	Preliminary evidence that belief regarding stimulus agency may modulate imitative compatibility effects. However, imitative compatibility effects were weak and the belief effect was extremely variable.

Table 33: Chapter 4 key findings and implications

Expt.	**Key findings**	**Implications**
7	Using a smaller focused go signal increased imitative compatibility effects in the group of participants who saw the focused flash first.	The focused flash increased attention to the stimulus movement, thus increasing imitative compatibility effects. In addition, the focused flash initially 'trained' them to pay attention to the stimulus movement.
8	No imitative compatibility present for the object stimulus prior to belief, however imitative compatibility effects were present for the object following the belief manipulation.	Provided evidence of a potential belief effect. However, the effect was contaminated by a Simon effect.
9	Pitted imitative compatibility against orthogonal spatial compatibility and the Simon effect. Initially observed orthogonal spatial compatibility/the Simon effect for the object stimulus. However, after instilling a human belief, imitative compatibility was present for the object stimulus.	Supports the theory that a human belief regarding stimulus agency modulates imitative compatibility due to the top-down knowledge that the movement was human generated and was not due to simply increased attention and SRC effects.

5.2 Attention

Attention has been a key theme throughout this thesis. Two key findings in the presented work emphasise the significance of attention in modulating the magnitude of imitative compatibility effects.

Firstly, the presented work supports the idea that imitative compatibility effects are susceptible to the general top-down attentional strategy of the participant that is implemented during movement observation. For example, a human bias of imitative compatibility effects was present in experiment 1a when participants were required to respond during the movement, but was absent when participants were required to respond after stimulus movement had occurred (Gowen et al., 2010). This key difference indicates that it is important to consider the attentional strategy of participants when designing automatic imitation paradigms. The current findings support the idea that in situations where the participant's on-going task does not occur concurrently with the irrelevant stimulus movement, attention to the movement may be reduced (or participants may potentially 'zone out' of the movement completely), thus reducing the distinction between biological and non-biological stimuli. This implies that visual attention to the irrelevant stimulus movement, at least to some degree, is required for differential imitative compatibility effects between stimulus types to be produced.

In addition, in experiment 7 we found that a smaller focused flash, which focused attention on the area in which the stimulus movement occurred, led to increased compatibility effects in the group of participants who saw the focused flash first relative to those who saw the diffuse flash first. This indicates that the focused flash trained participants to pay attention to the movement even in the diffuse flash condition. This implies that one's top-down attentional strategy can be altered depending on one's previous experience. The diffuse flash go signal may create a diffuse attentional mode, reducing attention to the stimulus movement. In contrast when attention is drawn towards the movement (focused flash) imitative compatibility effects are increased. This also suggests that 'attentional training' could potentially be used therapeutically to increase imitation. However, it should noted that these compatibility effects were contaminated with an additional Simon effect (in experiments 7 and 8) making it unclear to what extent the compatibility effects were driven by the Simon effect and to what extent they were driven by imitative compatibility. In experiment 9 (thumb up orientation), the observed imitative compatibility effects were reduced relative to experiments 7 and 8 due to the fact the contaminating Simon effect and spatial compatibility effects were removed.

The finding of an effect of attentional mode is in line with previous studies (Bach et al., 2007) which found that if attention is drawn away from the movement, imitative compatibility effects were reduced. In addition the idea that the magnitude of imitative compatibility effects, and thus MNS activation, is dependent on attention is in line with a recent EEG study. It was observed that stronger mu rhythm suppression occurred when observed grasping actions were relevant to the participant’s task (i.e. when they had to report how many times they had seen a particular grasp) as opposed to when the grasping actions were relevant (i.e. when the task was to report to a colour change of a cross which was located on the graspable object) (Schuch et al., 2010).

Secondly, the present work implies that automatic imitation (and thus the MNS) is modulated by attentional load and is therefore susceptible to capacity limit. In experiment 1b we demonstrated that imitative compatibility effects were removed by an easy visual secondary task. Imitative compatibility effects for the finger may have been absent in experiment 1b due to the fact that the oddball detection task was a) a visual task, thus may have occupied similar cognitive resources needed by the MNS to process the irrelevant movement and automatically activate the imitative response and; b) part of the participant’s top-down attentional strategy (whereas processing the irrelevant movement was not).

The idea that activity in MNS can be suppressed by a secondary visual task is in line with Chong et al.'s (2008) fMRI study in which participant’s observed irrelevant reach-to-grasp hand movements while performing a secondary visual discrimination task. They observed that activity in the left IFG was consistently reduced when performing a difficult visual discrimination task, while the activity in the IPL and STS was normal. Interestingly, however, the suppression of activity in the IFG only occurred when hand actions were observed, and did not occur when observing the non-biological dot movement. These findings indicate that the IFG might be specifically involved in ‘filtering out’ the processing of task-irrelevant human actions in conditions of high attentional load, allowing the ongoing task to be prioritised. The fact that the activity of the left IFG can be attenuated by a high cognitive load that limits attentional resources suggests that the activity of the MNS is not strongly automatic. The idea that human movements were completely filtered out is inconsistent with our results in experiment 1b, as participants correctly identified the oddball movements. The current findings therefore imply that when attention is drawn to a specific aspect of the observed movement, such as the kinematics of the movement, this may limit the ability process the overall direction of the movement thereby removing the imitative compatibility effect. The fact that activity in the IFG was suppressed specifically for biological stimuli is consistent with the finding in experiment 1b that while significant imitation for the finger stimulus was removed, automatic imitation for the object remained. Based on Chong et al.’s (2008) findings it is possible that the IFG is a key area for controlling which perceptual input gain access to the MNS. The current work extends the previous findings of Chong and colleagues (2008) because in their study, participants only passively observed actions but did not concurrently perform similar/dissimilar reach-to-grasp actions, therefore the point was raised that IFG attenuation in their experiment could not be conclusively attributed to the modulation of the level of MNs.

In contrast, when a secondary auditory task was used in experiment 2, imitative compatibility effects were produced for both the finger and object stimulus. Furthermore, we found that the compatibility effects for the finger stimulus were stronger when a dual auditory task was added relative to experiment 1a (where no dual task was added); although it should be noted that the larger compatibility effects in experiment 2 appear to be driven by the mirror view stimuli (suggesting an influence of spatial compatibility). This provides evidence that there may be a ‘baseline’ level of inhibition of imitation for the finger and the object stimulus. That is, when cognitive resources are not being occupied by a secondary task in a different sensory modality, they may be used for suppression of unwanted imitation. However, when both tasks involve the same sensory modality the results are consistent with a competition for shared cognitive resources, which the secondary visual task ‘wins’. When selective attention is divided between two tasks, stimuli compete for limited attentional capacity. When the total load of stimulus processing does not exceed this capacity, parallel processing may occur with little dual task interference. The secondary auditory task therefore did not exceed the total processing capacity, due to the fact the auditory task would draw on separate cognitive resources, and thus more efficient parallel processing would be permitted. Numerous studies support the idea that when there is a large amount of structural interference between two tasks (due to the tasks relying on the same neural mechanisms e.g. visual-visual), processing may sometimes occur sequentially in order to ‘share’ the common neural mechanisms and minimize loss of accuracy (Pashler, 1994).

The results of the work presented in experiments 1 and 2 are somewhat consistent with Lavie's (1995, 2005) account of general selective attention, which posits that there are two mechanisms of selective attention. The first mechanism is an early passive mechanism in which irrelevant stimuli will not be perceived or processed if there is insufficient capacity for processing them (high cognitive load). Therefore, the passive mechanism would result in decreased processing of the irrelevant stimuli in situations of high cognitive load (i.e. in the visual dual task due to the tasks sharing resources). The second mechanism involves active control of attention based on higher cognitive functions such as working memory and task co-ordination, which maintain attentional processing priorities such that low priority, irrelevant stimuli are actively rejected when perceptual load is low.

Due to the fact the active mechanism would draw on higher cognitive functions, in situations of increased cognitive load the capacity for active attentional control would be reduced, resulting in the increased processing of irrelevant stimuli. When the dual task accessed the auditory modality, it is likely that due to the dual task being in a different sensory modality, cognitive load was lower relative to experiment 1b (visual dual task). However, in line with Lavie’s model, the additional cognitive resources required to detect the auditory tone could reduce the capacity available for the active control of task priorities; thus increasing processing of the low priority irrelevant movements. The facilitation of imitative compatibility for the finger in experiment 2 relative to experiment 1a is therefore in line with Lavie’s perceptual load model which predicts that the increased cognitive load from the secondary auditory task may leave insufficient cognitive resources to actively suppress the perception of irrelevant stimuli, thereby increasing their processing. Increased processing of the irrelevant movements could explain the enhanced compatibility effects observed in experiment 2 relative to experiment 1a.

In experiment 1a when no dual task was added, imitative compatibility effects appear to be somewhat inhibited relative to experiment 2. This is in line with the fact automatic imitation effects have been documented when participants must attend to stimulus features to determine the required response e.g. attend to the colour of a hand in order to determine the required hand movement (Stürmer et al., 2000). It is known that simple colour discrimination tasks impose a low attentional load (Treisman and Gelade, 1980), thus based on Lavie's model, spare capacity may involuntarily 'spill over' to the perception of irrelevant stimuli. This suggests that with situations of low cognitive load, available 'residual' cognitive resources may involuntarily be allocated to the perception irrelevant stimulus movements (thus generating imitative compatibility effects in experiment 1a). However, there also could be a cognitive mechanism in line with Lavie's model that reduces 'interference' from perceived irrelevant movements, thus creating a baseline level of inhibition in experiment 1a, as long as cognitive resources are available to maintain the current attentional priorities (i.e. responding to the go signal).

A recent study by Cross and Iacoboni (2014) has provided novel neurophysiological evidence that control of imitative tendencies (i.e. inhibition of inappropriate or unwanted imitation) occurs through MNS modulation. They used TMS to measure corticospinal excitability during an imitative compatibility task. The colour of the border surrounding an image of the hand stimulus in a neutral position coded the 'preparatory condition', whereby a green colour border indicated that participants should prepare to imitate the movement and a red border indicated the participant should prepare to counter-imitate the movement. There was also a 'no preparation' condition in which a black border was shown initially. In this condition participants did not know the appropriate mapping until the onset of the target video, when the black border changed to either a red or green border. In addition, they obtained a baseline measure of motor resonance in a task using similar two choice motor preparation task demands but with the influence of SRC removed. They found that motor resonance was similar to baseline during preparation to imitate, and lower than baseline during the counter-imitation and unknown mapping conditions. They interpreted this data such that preparatory processes inhibit imitative responses when the response it is likely to conflict with task goals. Interestingly, Cross and Iacoboni's (2014) findings are in line with the predictions of cognitive models of SRC, which suggest it is possible to strategically suppress SRC when the response is likely to interfere with task goals (de Jong, 1995). Such models suggest that suppression occurs in preparation for incompatible responses (when the stimulus–compatible response is incorrect) and in preparation for trials in which the required stimulus–response mapping is unknown prior to movement (as in experiment 1a). This suppression manifests behaviourally as reduced compatibility effects, as the compatible response no longer benefits from automatic response activation making compatible and incompatible RTs similar. These findings are of particular relevance since the existence of an inhibitory mechanism which suppresses imitative compatibility effects in situations where the mapping condition is unknown supports our interpretation of the imitative compatibility effects in experiment 1a occurring relative to a baseline level of inhibition.

While the auditory dual task may have allowed for parallel processing of the irrelevant movement and automatic activation of the imitative response to occur, cognitive resources for differentiating between biological and non-biological stimuli and inhibiting imitation may be limited. On the other hand, in experiment 1a where no dual task is used, additional resources may be available to differentiate between biological and non-biological stimuli, causing a ‘human bias’ to be present. This interpretation implies that the differentiation element may involve a higher cognitive level of processing, and therefore may not occur unless cognitive resources are available. Therefore, reduced attention to the stimulus movement or reduced attentional resources in a dual task situation may cause a lack of differentiation between biological and non-biological stimuli, thus producing similar imitative compatibility effects. It is possible that discrepancies in the literature regarding whether or not there is a human bias of imitative compatibility could reflect differences in top-down factors such as attention and cognitive load between different experiments. This interpretation is also consistent with Gowen and Polikoff’s (2012) model of mimicry (described in **section 1.8**) which suggests differentiation between biological and non-biological stimulus types may be an active process which requires attentional resources. It is known that perceptual and cognitive (e.g. working memory) tasks use different resources from those involved in the selection and execution of action (Isreal et al., 1980). Therefore, when cognitive load is high, differentiating between stimulus types may not be prioritised, and imitative compatibility effects may occur unmodulated via the visomotor route.

The presented work indicates that a highly focused attentional state in which attention was highly focused on the goal of detecting oddball movements (i.e. a detailed aspect of the kinematics of the movement) in experiment 1b resulted in insufficient capacity to process the direction/type of movement, thus removing automatic activation of the imitative response. The current findings suggest that after an irrelevant movement has entered conscious awareness, if attention is focused on detecting a particular aspect of the movement (increasing cognitive load and decreasing attention to the overall direction of the movement), this can subsequently suppress the activity of the MNS (thus suppressing the automatic activation of the imitative response). The fact that imitative compatibility effects were removed even though the secondary task involved attending to the same spatial location as the observed movement, suggests that focused attention on a different feature of the action (i.e. its kinematics) can remove imitative compatibility. This implies that the different features of an action (e.g. kinematic, biological origin, direction etc.) may be processed separately; and the most relevant features may be prioritised when attentional resources are limited. This is consistent with the fact that different cortical areas have been implicated in processing different aspects of a movement. For example, evidence indicates that the primary motor cortex encodes the direction of movement (Toxopeus et al., 2011) while the supplementary motor area is involved in transforming kinematic information into dynamic information (Padoa-Schioppa et al., 2002). Chong et al., (2008) results are also consistent with experiment 1b. They found that automatic imitation of grasp was eliminated by attending to a different aspect of a stimulus in the same spatial location (i.e. the laterality of the stimulus or a colour diamond appearing on the stimulus) as opposed to attending to the grasping movement itself (Chong et al., 2008).

The presented work adds to existing evidence of increased imitative compatibility effects/MNS activation during dual task conditions (Muthukumaraswamy and Singh, 2008; Saucedo Marquez et al., 2011; van Leeuwen et al., 2009a) using a variety of techniques. For example, in support of a facilitatory effect of cognitive load in a different modality, Kühn and Brass (2008) found that automatic imitative responses to a hand stimulus were much less slowed relative to symbolic stimulus when participants had a secondary task of articulating a word continuously during an automatic imitation task. This provides evidence that a dual task involving speech production had a facilitatory effect on imitation. Saudeco-Marquez and colleagues (2011) discussed the possibility that increased M1 excitability observed in dual task conditions might be explained by findings that the excitability of hand muscles increases when one is required to put items in an ordered series e.g. during counting (Andres et al., 2007). This explanation could also potentially be applied to Muthkumarswamy and Singh’s results due to the tasks involving counting/sequences. Importantly, the current results do not support this view, as the secondary auditory task used in the current study did not require any form of counting or other sequential processing of the order of a series of elements, yet our results indicate a potential disinhibition of imitative compatibility effects. It is therefore more likely that as suggested by Van Leeuwen et al. (2009), and in line with our current interpretation, increasing cognitive load might occupy cognitive resources necessary for the control/inhibition of imitation. Saudeco Marquez et al. and Muthkumarswamy and Singh’s results might therefore be indicative of a disinhibition of the motor system in situations of high cognitive load. Van Leeuwen and colleagues (2009) found that increasing working memory load (with a task that would be classed as auditory as opposed to visual) facilitated RTs for finger movements, and argued that the fact that facilitation of imitative processes under situations of high cognitive load suggested behavioural imitation is extremely automatic in nature. However, we have demonstrated that when cognitive resources required for the dual task overlapped with those required to produce imitative compatibility effects (i.e. visual resources), imitation was removed, indicating that the facilitation of imitative compatibility effects is dependent on the sensory modality of the dual task. This argues against the automaticity of imitative compatibility effects.

A hallmark of automatic processing is that it operates without drawing on general cognitive resources (Pashler, 1998). If ‘automatic’ imitation were a truly automatic process we would expect it to 1) not draw on general cognitive processes; 2) be immune to modulation by top-down mechanisms such as attention; and 3) occur rapidly and automatically without interfering with other tasks. The discrepancy between the results of experiment 1a and Gowen et al (2010) indicates that attention to the stimulus movement is required to produce automatic imitation effects, and that automatic imitation is susceptible to one's attentional strategy during movement observation. Furthermore, in the dual task experiments (1 and 2) we found an effect of attentional load which is dependent on the sensory modality of dual task. Consistent with the view that few cognitive processes, if any, are entirely independent of selective processes (Kahneman and Treisman, 1984; Logan, 1980), these findings suggest automatic imitation is not a strongly automatic process. Based on these findings, automatic imitative processing of hand stimuli can be seen as both similar and different to related processes such as those involved in processing emotional facial stimuli. For example, in contrast to our current findings of a strong influence of attention on automatic imitative processing of hand stimuli, processing of emotional facial stimuli occurs seemingly automatically (i.e. being relatively resistant to attentional control). However, in line with current findings of an effect of attentional load, Pessoa and colleagues (2002) found that the emotional facial stimuli were only processed when attentional resources were not occupied by an attentionally demanding competing task.

Clearly, the automatic imitation paradigm used in the current thesis is highly simplified in comparison with mimicry in a naturalistic social setting. However, given that is assumed that the underlying mechanisms are the same our findings regarding the influence of attention might also have implications for theories of mimicry. The current results support the existing view that we have a strong tendency to unconsciously mimic the actions of others, and that such mimicry may be typically controlled by a baseline level of inhibition. For instance, in healthy adults the potential to imitate observed actions is not always automatically translated into overt imitation. In our everyday lives a huge number of actions are constantly occurring in the world around us, however, only a small proportion of these observed actions are behaviourally relevant. Furthermore, there are clearly situations in which it would be beneficial to suppress imitation of an observed action (e.g. if the observed action is socially or contextually inappropriate or in situations where goal-directed action is required and is different from the observed behaviour).

We have found a strong influence of attention on imitative compatibility effects, thus our results are in line with the idea that greater visual attention to one's social environment and the actions of others would generally increase mimicry. This fits in with the 'attentional hypothesis' has been proposed by van Baaren et al. (2003), who suggested that an 'independent self-construal' (minimizing the influence of others on the self) leads to increased attention towards oneself and reduced attention towards others, thus fewer mannerisms of others would be observed, decreasing the likelihood of mimicry occurring. Similarly, Lakin and Chartrand (2003) argued that the desire to affiliate with others might cause more attention to be paid to what is occurring in one's social environment, thus allowing one to perceive more. This may ultimately result in a stronger relationship between perception and behaviour. These theories suggest that when one develops rapport and feels comfortable and interested during a social interaction, one would be more inclined to focus attention on the interacting partner more; therefore the potential for motor mimicry may be increased. Conversely, when ones dislike the interacting partner or feels uncomfortable in a social interaction, greater attention may be focused on oneself, reducing the potential for motor mimicry.

In summary, the presented work indicates that top-down attention exerts a strong influence on imitative compatibility effects in a variety of ways. Imitative compatibility effects are sensitive to 1) the *location and level of attention* (e.g. when attention is highly focussed on a particular aspect of the movement in oddball trials), 2) the participant's *attentional mode or strategy* (as shown by the difference between experiment 1a vs. Gowen et al. (2010) and the focused vs diffuse flash), and 3) overall *attentional/cognitive load* (as shown by a dual task approach in experiments 1b and 2). We have found that imitative compatibility effects are sensitive to general top-down attentional strategy. If attention to the movement is not required (i.e. when the go signal is presented after the movement in Gowen et al., 2010) or a diffuse attentional mode is created (e.g. diffuse flash), attention to the stimulus movement may be reduced, thus diminishing or removing imitative compatibility effects. However, we have also shown that in line with Chong et al. (2009) and Bach et al.'s (2007) findings, automatic imitation is also contingent on participants attending to the feature of the observed hand that was relevant to their responses (i.e. movement direction/type as opposed to kinematics). These findings imply that automatic imitation can be removed by closely attending to a different feature of the movement. The present work has also provided evidence imitative compatibility effects (and thus the activity of the MNS) is modulated by attentional load and therefore is susceptible to capacity limit. In the context of the discussed literature, the presented work is consistent with the following explanation of the effects of cognitive load on imitative compatibility effects: 1) when no dual task is added cognitive resources are available for processing of irrelevant stimuli and actively controlling task priorities, causing a baseline level of inhibition and 'human bias' (experiment 1a); 2) a secondary visual task, regardless of difficulty, drains the cognitive resources available to facilitate imitative compatibility effects, due to the fact both tasks share similar cognitive resources (visual); 3) when cognitive load is relatively lower in the auditory task (due to the dual task being in a different sensory modality) imitative compatibility effects are produced. However, a facilitation of MNS activity may occur due to the dual auditory task occupying cognitive resources required for the active control of imitation.

Overall, the presented work adds to accumulating empirical evidence (Chong et al., 2009, 2008; Gowen et al., 2010; Bach et al., 2007) and current models of mimicry (Gowen and Poliakoff, 2012; Wang and Hamilton, 2012) which suggest that top-down attention exerts a strong influence on imitative compatibility effects, thus implying that the imitative compatibility effects are not entirely 'automatic'.

5.3 Belief regarding stimulus agency

Two key findings presented in the thesis demonstrate that prior knowledge/beliefs regarding stimulus agency modulate imitative compatibility effects for non-human stimuli. Firstly in experiment 9, we conclusively demonstrated that explicitly instilling a top-down human belief regarding stimulus agency influenced participants' responses such that the object stimulus was imitated as if it were a human finger movement. Secondly, the results of experiments 3 and 4 support the idea that imitative compatibility effects might be modulated by the participant's own implicit beliefs regarding stimulus agency, without any explicit instructions being given. This indicates that it is important to consider possible carry-over effects of belief regarding agency when comparing automatic imitation for human vs. non-human stimuli. These key findings will now be discussed in further detail.

Arguably the most interesting result presented in this thesis is the finding that when participants were instructed that the movement of the object was generated from a human finger movement, the belief instructions had a top-down influence participant's responses to the object stimulus. In the belief condition the object movement was consequently treated as if it were human finger movement, and thus imitative compatibility effects were produced. One likely explanation for this effect is that in the belief condition participants might imagine the object movement as if it were a human finger movement, leading to the activation of MNs and hence imitative compatibility effects. This interpretation is supported by the fact that imagined movements have been shown to activate motion processing areas (Ruby and Decety, 2001). In addition, MN studies in macaques show that MNs remain active when the end point of the action is occluded (Umilta et al., 2001) or during the momentary occlusion of the experimenter and other moving objects behind a screen (Baker et al., 2001), suggesting the MNS can code for 'inferred movement' of stimuli that are no longer in sight. What makes these results particularly convincing is that initially prior to instilling a human belief, the compatibility effects produced for the object stimulus movements were not attributable to imitative compatibility effects, but were generated by spatial SRC effects. This is important because previous studies which have investigated the effects of belief in automatic imitation have not generally controlled for spatial compatibility effects. In addition, based on the current work it is probable that previous studies that have reported imitative compatibility effects for object stimuli, in the absence of any implicit or explicit belief that the object represents a human movement, the compatibility effects observed are likely attributable to spatial SRC effects.

As discussed in **section 1.7.3**, the success of such belief manipulations appear to depend on the ambiguity of the non-human stimulus used, such that that the belief manipulation is more likely to be successful when manipulating belief regarding an ambiguous non-human stimulus (dot or other abstract object, e.g. Stanley et al., 2007) as opposed a stimulus which clearly appears to be either human or non-human (e.g. gloved hand/robot, e.g. Liepelt and Brass, 2010; Press et al., 2005). In line with this idea, Press (2011) argued that *'belief about identity may have greater impact when there is less* *perceptual information upon which to base inferences'.* As the moving blue rectangle is an ambiguous/abstract stimulus, we hypothesized that participants would find it plausible to believe that the movement of the rectangle was generated by a human finger movement. In line with our predictions, participants completely altered their pattern of responding to imitate the object as if it were a human finger movement in the belief condition, even though the object stimulus was physically identical in the object condition, where only spatial compatibility effects were present.

The current work is in line with Liepelt and colleagues' (2008) proposal that some of the imitative compatibility effect is driven by the attribution of intention, rather than by the movement itself. Liepelt and Brass (2010) 'gating hypothesis' explanation regarding how belief might modulate imitative compatibility proposes that only when an observed movement is believed to be human generated (intentional) does the movement gain privileged access to the MNS. Conversely, when the movement is thought to be generated by a non-intentional agent, the movement does not gain access to the MNS. The current work extends Liepelt and Brass (2010) previous findings, which showed a modulating effect of belief on imitation using a between-participant design, as the current work has used a within-participant design, showing that the belief effect cannot be accounted for by inter-individual differences between different groups of participants.

Several of the experiments presented in this thesis support the notion that the human MNS is tuned to respond to the observation of human motion, or movements that are believed to be human generated, to a greater extent than non-human movement or unintentional movement. Firstly, in experiment 1a we replicated previous findings of stronger imitative compatibility effects for the biological relative to the non-biological stimulus. Secondly, in experiment 9, we found that imitative compatibility effects were present for the human hand stimulus, while only spatial compatibility effects were present for the object prior to the belief manipulation. Furthermore, the fact that imitative compatibility effects were present when the object movement was believed to represent a human movement, suggests that a human belief regarding stimulus agency up-regulates activity of the MNS causing non-biological stimulus movements to be imitated in a similar way to human movements. The effect of belief regarding agency observed in experiment 9 indicates that even abstract non-human stimuli such as a moving rectangle can potentially elicit imitative compatibility effects equivalent to those produced for a human stimulus if the non-human movement is believed to be human generated. These findings imply that the MNS can be also activated by non-human stimuli believed to be generated by a human movement, and in such cases the movement of the non-human stimuli is processed as if it were a human movement.

This is in line with the fact that the STS is also responsive to the observation of point light displays representing human movements (Grèzes et al., 2001; Grossman et al., 2000). Similarly, non-biological stimuli have been shown to induce activity in the STS if the inanimate object was attributed a mental state, as if it were animate (Castelli et al., 2000).

The fact that abstract stimuli can activate the STS suggests that it is also responsive to movements believed to represent human or intentional movement, rather than specifically to the observation of human movements. Some researchers posit that biological tuning of the MNS may be important for socio-cognitive functioning (Gallese and Goldman, 1998), and MNS activation may indicate the extent to which a non-human stimulus is considered a 'social interactor' (Chaminade and Cheng, 2009). It has been suggested that when the MNS is active during the observation of non-human agents such as humanoid robots, this may be due to attributing of characteristics associated with humans, such as mental states, feelings and intentions to non-human stimuli (Chaminade and Cheng, 2009). Interestingly, Tsai et al., (2008) found a joint Simon effect (i.e. a spatial compatibility effect that occurs when two people complete complementary components of a Simon task) was present when participants thought that they were interacting with another person in a different room. Similarly, Tsai and Brass (2007) provided evidence that a joint Simon effect only occurred when participants co-acted with another person and disappeared when participants interacted with a wooden hand. However, in a later study, participants watched a video of either the human or wooden hand, in order to increase the perceived agency of the wooden hand stimulus (Müller et al., 2011). They found that participants who watched the human hand only showed a joint Simon effect while interacting with a human hand, while those who watched the wooden hand video showed a Simon effect only when co-acting with the wooden hand, indicating that motor simulation strongly depends on higher order processes. In this way, automatic imitation and joint action mechanisms may be similar in the sense that the magnitude of the effects seem to be driven by beliefs about the agency of the stimulus or co-actor.

Secondly, the results of experiments 3 and 4 suggest that the modulation of imitative compatibility effects by belief regarding stimulus agency can occur without any explicit knowledge regarding the agency of the stimulus being given; but rather due to the participant's own implicit beliefs. Gowen and Poliakoff (2012) suggested that the fact that compatibility effects are more likely to be significant for a non-biological stimulus, when stimuli are presented in pure blocks as opposed to mixed within a block of trials, might be due to differences in attention (i.e. more attention may be drawn to stimulus differences in a mixed stimulus presentation condition). However, the fact that we found that imitative compatibility effects for the object stimulus were present only in the group of participants that observed the finger stimulus first, supports a new implicit belief explanation for this observation. The current work suggests that when no information is explicitly given regarding the agency of an ambiguous non-biological stimulus, imitative compatibility effects may be inhibited or suppressed by default when stimuli are presented mixed within a block of trials. Furthermore, we have found that compatibility effects for non-biological stimuli which neither look human, nor are believed to be human generated, are attributable to spatial SRC effects, and not imitative compatibility effects. When stimuli are presented in separate blocks, however, imitative compatibility effects for the object stimulus may be attributable to the group of participants who observed the human stimulus first, due to participant's creating an implicit belief regarding the agency of the object movement based on the previously observed human movement. The human agency of the previously observed finger movement therefore appears to carry over to the object stimulus in this group of participants.

This has wider implications for the interpretation of the results of previous studies. For example, Jansson and colleagues (2007) reported a similar compatibility effect for tapping or lifting a pen compared with tapping and lifting of a finger. Likewise, they found equivalent compatibility effects for a pair of dots contracting and expanding as for a hand stimulus opening and closing. Based on these results they suggested that previous findings of imitative compatibility effects might be better explained by 'conceptual SRC effects'. Furthermore, they suggested that such effects could be achieved equally for biological and non-biological stimuli whenever the salience of stimuli is controlled for. This interpretation is presumptuous in itself, as it is equally plausible the effects observed could represent imitative compatibility for the biological stimulus, and spatial compatibility for the non-biological stimulus. However, the current work offers a potential alternative interpretation of their findings. Although their biological and non-biological stimuli were presented in separate blocks and the order of presentation was counterbalanced, their statistical analysis did not account for possible carry-over effects of seeing the biological vs. the non-biological stimulus first. Based on the current results, it is conceivable that the effects they observed for the non-biological stimulus may have been driven by the group of participants who saw the biological stimulus first, whereby there was a carryover effect of human agency from human finger/hand movement to the pen/dots.

The results of experiment 9 indicate it is likely that imitative compatibility effects were present for the finger stimulus and the object stimulus in the 'biological stimulus first group', while spatial compatibility effects might be responsible for compatibility effects observed for the object in the 'non-biological stimulus first group'. These findings could equally be applied to any paradigm in which biological and non-biological stimuli have been presented in separate blocks of trials, indicating the importance of further investigating carry-over effects between sub-groups of participants. These results suggest that caution should be taken when comparing compatibility effects between biological and non-biological stimuli presented in separate blocks, as it is possible that compatibility effect for non- biological stimuli may be based on a carry-over effect in the sub-group of participants who previously observed the human stimulus.

These findings imply that imitative compatibility is highly susceptible to subtle cues as although no explicit information was given, participants may form implicit beliefs regarding the non-biological stimuli based on the prior experience of seeing a similar human movement. Forming such a belief is plausible given that in most cases, the non-biological stimulus is created to closely match the biological stimulus in terms of shape and surface characteristics, luminance and kinematics, leading to obvious similarities. Interestingly, this effect only seems to occur when the participants have seen the hand first, but not in the mixed condition, supporting the idea that participant’s may inhibit compatibility effects for the object in the mixed condition.

In addition, it is also worth considering whether any effects observed in ‘non-biological stimulus first’ subgroups of participants could be due to implicit beliefs that the non-biological movement was meant to represent the human movement that they were asked to perform. In the current paradigm, it is unlikely that participants in the non-biological first group would associate the left-right movement of the object with the pressing or releasing response, and in line with that we found no effects of imitative compatibility in the object first subgroup. However, it is possible that the choice of stimulus in some previous studies may have increased the chance of implicit beliefs regarding the non-biological stimulus to be formed (even in the non-biological first group). For example, Jansson et al.’s (2007) choice of pen/dot stimuli had obvious similarities to the actions that participants were being asked to perform.

Overall, the current results support the idea that the MNS is tuned to respond to human movements that physically appear to be human, as well as non-human movements that are believed to be human generated. This supports the idea that only movements that are believed to be intentionally produced gain access to the MNS (Liepelt and Brass, 2010), and indicates that the MNS is susceptible to the top-down influence of belief/prior knowledge regarding stimulus agency. Importantly, the effect of belief as well as the strong influence of attention shows that the MNS is highly susceptible to top-down influence. These findings fit in with a number of current models of mimicry (discussed in **section 1.8)** which suggest that mimicry requires higher brain systems beyond the MNS (Southgate and Hamilton, 2008; Wang and Hamilton, 2012; Gowen and Poliakoff, 2012).

5.4 No apparent relationship between imitative compatibility effects and self-reported measures of empathy

The current work does not support a consistent relationship between imitative compatibility of finger or object movements and empathy. While we have looked at the relationship between these factors throughout this thesis and attempted to control for spatial compatibility effects, only in experiment 9 was there a clear dissociation between spatial compatibility effects and imitative compatibility effects. The fact that no significant correlations were present in experiment 9, which measured pure imitative compatibility effects, indicates that the proposed relationships between these factors might not exist. There are four main explanations which may have contributed to this null finding, which will be discussed below.

Firstly, as discussed in **section 1.9.3**, while there is a great deal of theoretical support for a relationship between empathy and imitative abilities (Gallese and Goldman, 1998), the empirical evidence to support such a relationship is lacking (Baird et al., 2011). It is therefore possible that such a relationship might not exist at all.

Secondly, it is plausible that a relationship between imitation and empathy might only exist for emotional stimuli (i.e. emotional facial stimuli) as opposed to non-emotional stimuli (i.e. hands/objects). As discussed by Hess and Fischer (2013), while mimicry of emotional facial expressions has commonly been assumed to be equivalent to mimicry of other behaviours (such as foot tapping for example); these forms of mimicry differ in that emotional facial expressions are, in contrast to most other non-verbal behaviours, intrinsically meaningful, providing information about the persons disposition or intentions. It is therefore also possible that a relationship between imitative compatibility effects and empathy might only be present for emotional stimuli, such as emotional facial expressions. A number of studies have reported correlations between empathy and imitation of emotional facial expressions (Harrison et al.,2010; Sonnby–Borgström, 2002). One recent study found that highly empathetic participants tended to mimic a hand stimulus assigned with a high reward value relative to a hand assigned a low reward value; however they found no correlation between individual trait empathy and mimicry for human or robotic hand actions stimuli once collapsed across the high/low reward conditions (Haffey et al., 2013). The fact that a relationship between empathy with hand imitation only occurred when a reward value was assigned suggests that imitation of hands may not be intrinsically rewarding.

Thirdly, the lack of correlation between these factors could be due to the known limitations of using self-reported questionnaire measures to measure empathy. Self-report measures do not offer an objective measure of empathy, therefore it has been argued that the reliability and validity of such measures is questionable (Chlopan et al., 1985). Self-report measures of empathy are also vulnerable to intentional biases, such as social desirability, which may influence the truthfulness of responses (Duan and Hill, 1996). For instance, Kämpfe et al., (2009) observed that empathy (as measured by self-report measures) was higher in delinquent participants relative to non-delinquent participants. However, they found that the delinquent participants had a weaker implicit association between empathy and positive compared to empathy and negative concepts. Thus an indirect measurement of empathy indicated that empathy was actually higher in the control participants relative to delinquent participants. This highlights the fact that caution must be taken when using self-report measures of empathy.

Whether or not questionnaire measures are appropriate for measuring the different components of empathy remains an open question. While empathy has traditionally been measured using self-report measures, due to their known limitations, psychophysiological methods such as (neuroimaging, EEG, EMG, and heart rate for example) are increasingly beginning to be used to more objectively measure of changes in nervous system activity associated with empathy (Neumann et al., 2011). Such methods could be used to broaden our understanding of empathy, as well as providing a complimentary approach to devise new scales for measuring empathy or to validate existing self-report measures.

In addition, it has also been noted that somewhat surprisingly, different empathy questionnaires measures proposed by different authors do not tend to inter-correlate with one another (Levenson and Ruef, 1992). This lack of correlation between different measures of empathy might indicate that people are generally incapable of introspecting about their own empathetic ability. However it is also likely to reflect the fact that there is little agreement on a definition of empathy, and therefore different questionnaires actually measure completely different facets of empathy.

Empathy is a very complex and multifaceted construct. A number have studies have challenged the notion that empathy is a unitary concept (as proposed by Baron-Cohen and Wheelwright, 2004) and have begun examining different forms of empathy. As discussed in **section 1.9.3**, it is generally agreed that there are two distinct components of empathy: cognitive empathy and affective/emotional empathy. In line with this, Shamay-Tsoory et al. (2003) observed that deficits in emotional empathy occurred after damage to the IFG, while deficits in cognitive empathy were related to ventromedial prefrontal cortical damage, indicating that the neural substrates for cognitive empathy and emotional empathy are dissociable.

The various self-report questionnaire measures of empathy reflect the multiple different possible definitions of empathy. For example, Hogan’s empathy scale (Hogan, 1969) measures cognitive empathy while Mehrabian and Epsteins’s questionnaire of emotional empathy (QMEE; Mehrabian and Epstein, 1972) defines empathy in terms of affective empathy. While the EQ treats empathy as a unitary concept, Davis’s Interpersonal reactivity index (IRI; (Davis, 1983) scale includes both cognitive and affective components, and has therefore been more recently preferred by some researchers due to the fact it assigns a separate score for each of the four distinct components (perspective taking, empathetic concern, personal distress and fantasy).

Therefore, fourthly and finally, the fact we have not found a correlation in this study, might suggest that imitation is better related to certain components of empathy (e.g. perspective taking) as opposed to empathy as a unitary concept. A number of lines of evidence suggest that the processes of mimicry and visual perspective taking are linked (Spengler et al., 2010b; Santiesteban et al., 2012a). Future studies could include Davis’s IRI ‘perspective taking’ subscale to examine this hypothesis. Interestingly, it has been observed that children with ASC who displayed less empathy were less likely to experience the rubber hand illusion - an illusion in which perceived hand ownership can be transferred to a rubber hand following synchronous visual and tactile stimulation (Cascio et al., 2012). This supports the idea that empathy is related to the ability to allow multimodal stimulation to induce a feeling of body ownership of the rubber hand. Some scholars argue that differentiation of self from other and having a sense of body ownership are precursors to imitation and empathy (Chaminade et al., 2005).

On the other hand, Smith (2006) posits that is possible that cognitive and emotional empathy are separate, complementary systems that may function separately or may be used in an integrated way. Smith's (2009) empathy imbalance hypothesis of autism suggests that people with ASC may have low cognitive empathy but high affective empathy. This hypothesis is in line with recent findings that individuals with ASC have reduced pain thresholds and increased empathetic arousal in response to observing body parts being accidently injured; but decreased responses when viewing a person purposefully injuring another person (suggesting impaired understanding, or perception of, others' distress).

In conclusion, the current work cannot support the hypothesis that there is a relationship between self-reported empathy and imitative compatibility effects for finger (or object) movement stimuli. However, existing research in this area indicates that the relationships between these factors may be extremely complex, and extensive research will be required to fully understand these relationships. For example, Baird et al., (2011) pointed out that to date there have been no fMRI studies investigating empathy that use an automatic imitation task, which represents a significant gap in our knowledge. Future studies should seek to further understand the relationship between empathy, ASC, and various components of imitation, such as perspective taking and their neural correlates. Further clarification is needed on this issue, as it is not known which types of imitation (voluntary vs. automatic), which types of imitative stimuli (emotional vs. non-emotional: i.e. hand, body, face) and which components of empathy (cognitive/affective) or sub-components of empathy such as (perspective taking or personal distress) are related to one another. It is also still currently unclear to what degree the different components of empathy are separable, and furthermore which of the separate components are impaired in ASC. Systematically investigating these factors using psychophysiological methods will help in developing methods capable of measuring these components. This will allow us allowing us to conclusively determine whether or not such relationships exist in future studies.

5.5 Implications and Future Directions

5.5.1 Future studies in ASC

The ultimate aim of this research was to develop a paradigm which could be used to directly test the top-down modulation hypothesis of autism in ASC populations. Directly testing this hypothesis would be useful in disambiguating the opposing proposals of the broken mirror theorists and supporters of the top-down modulation hypotheses of ASC. In the current thesis we did not find a consistent relationship between imitative compatibility effects and autistic traits; however this may be due to the lack of variability in autistic traits in the neurotypical participants recruited to produce an effect. Therefore, directly testing the top-down modulation hypothesis in participants with ASC relative to controls could further our understanding of the relationship between imitation and ASC.

There are a number of findings based on the presented work that would be interesting to investigate in populations with ASC. Keysers and Gazzola (2014) have suggested that a lack of social motivation and reduced attention to social stimuli may be key to understanding reduced levels of empathy and impaired social interaction in ASC. Autistic individuals are known to show impaired social gaze (Pelphrey et al., 2002) and eye contact (Senju and Johnson, 2009). Furthermore, individuals with ASC fail to show preferential sensitivity to social vs non-social cues (Senju et al., 2004). Interestingly, Neumann et al. (2006) found that bottom-up attentional processing was intact, and that abnormal top-down modulation of attention for faces drove the bias for fixating on the mouth as opposed to the eyes in individuals with ASC. They suggested that the abnormal top-down modulation for saccades made to the mouth could be part of a with a neurodevelopmental progression in which infants with ASC fail to direct attention to faces and eyes due to abnormal reward circuitry (Dawson et al., 2005) or to abnormal circuitry for emotional salience (Schultz et al., 2005). It is therefore possible that a lack of attention to biological movement relative to non-biological movement may lead to abnormal top-down modulation of automatic imitation. If top-down attentional processing is abnormal in ASC due to reduced social motivation, one might expect the human bias of automatic imitation for the finger vs. the object stimulus to be reduced or absent in ASC. This could be established by carrying out a ‘control’ version of the imitative compatibility task using the ‘thumb up’ rotated version of the paradigm used in experiment 9, presenting stimuli randomly intermixed within a block of trials as in experiment 1a. If there is a significantly reduced human bias in the ASC group compared to matched controls, this would support the idea that less priority is given to human stimuli in ASC.

One of the most interesting studies which could be directly carried out in ASC would be using the ‘thumb up’ condition of the orthogonal paradigm in experiment 9 while manipulating belief regarding the agency of the object stimulus in participants with ASC. This would allow us to directly test the top-down modulation hypothesis of ASC. We might expect to see orthogonal spatial compatibility for the object) and imitative compatibility for the hand stimulus (if imitative compatibility is intact in ASC until required to modulate that imitation). However, if, as hypothesized, top-down modulation of imitation in the belief condition is impaired in ASC such that imitation is not influenced by belief regarding agency, this would provide strong evidence to suggest that top-down modulation of automatic imitation is atypical. One consideration when using rotated thumb up paradigm would be to recruit left-handed participants in future experiments in order to further increase the compatibility effect, as one would expect the compatibility effect to be larger when using ones dominant hand. Fortuitously, an increased incidence of left-handedness in ASC relative to the neurotypical population is well documented in the literature (Gillberg, 1983; Leboyer et al., 1988). The current rotated paradigm can also disambiguate whether previous reports of hyperimitation in ASC (Spengler et al., 2010a) was a true effect. Given that the effects reported were not fully dissociated from spatial compatibility, as stimuli were presented from a mirror view, the results could be due to an increased spatial compatibility effect in the ASC group. Using the orthogonal paradigm as in experiment 9 (thumb up orientation) would help to clarify this issue.

Similarly, it would also be interesting to see if an implicit carry over effect of human agency to the object stimulus in the 'finger first' group when stimuli are presented in separate blocks in participants with ASC. A lack of a carry-over effect would indirectly indicate impaired top-down modulation, as it would indicate participants with ASC do not use prior knowledge/experience in the same way that neurotypical participants appear to be doing.

Future studies could also seek to determine whether individuals with ASC have the same 'baseline' inhibition of imitative compatibility/mimicry that appears to be present in experiment 1a (as compared to experiment 2). If there is no baseline level of inhibition in ASC, this may explain reports of hyperimitation that have been described in a number of mimicry studies in participants with ASC. If individuals with ASC do not have a baseline level of inhibition, and/or are unable to appropriately modulate levels of imitation during social interactions, this may explain some of their difficulties in social interaction.

Interestingly, it has been observed that children with ASC performed better than neurotypical children in a task involving mental rotation of objects, but performed worse in a visual perspective taking task (Hamilton et al., 2009; Soulieres et al., 2011). Similarly, a recent study has found that participants with ASC did not show the usual advantage for mentally rotating hand stimuli in physically comfortable positions relative to physically awkward positions during hand laterality judgement tasks i.e. individuals with ASC have an 'enhanced' ability to mentally rotate stimuli in biomechanically awkward positions (Conson et al., 2013). They suggest that the atypical ability to mentally rotate hand stimuli in ASC might correspond to the fact individuals with ASC perform poorly on visual perspective taking tasks. For example, Kessler and Wang (2012) found that individuals with low autistic traits (as measured by the AQ questionnaire) were more prone to mentally adopt the spatial alignment of another person's body than those with high autistic traits, who might be more likely to adopt alternative strategies such as object rotation rather than embodied processing to solve hand laterality tasks. Since the hand laterality task implies mental simulation of hand movements that are not goal-directed i.e. requires mental imagery of meaningless and goal-less actions, they suggest that the fact that mental rotation of goal-less movements is abnormal in ASC might be line with their impairment in goal-less imitation. Therefore, if our assumption that the messy results of the thumb down orientation is due to difficulty with mentally rotating the stimulus, and participants with ASC have an enhanced capability to rotate stimuli in biomechanically awkward positions, then we would expect to see a larger imitative compatibility effect to be present in the thumb down orientation as the effect would represent the effects of imitative compatibility and spatial compatibility/Simon effect combined.

It is also possible that impaired inhibition in ASC could be linked the impairments in executive function that have been documented in ASC (see Hill, 2004 for a review). Inhibition is a component of executive function which allows one to inhibit prepotent responses or ignore distracting stimuli in order to withhold actions that are inappropriate in a given social situation. Inhibitory functions are thought to depend on the activity of the prefrontal lobe, due to the fact as previously discussed patients with prefrontal lobe damage are commonly impaired in inhibition of imitation (Shallice and Burgess, 1991). A number of observations in ASC are suggestive of difficulties in inhibition, for instance, the repetitive and stereotyped behaviours that are characteristic of the disorder. Interestingly, a recent study has found that children with ASC show intact inhibition in the classic Stroop task and response inhibition stop signal task; however were significantly impaired in resistance to distractor inhibition (Adams and Jarrold, 2012). In light of the current findings, it is possible that problems with modulating imitative compatibility could be linked to impairments inhibition of ‘distractors’ i.e. the irrelevant stimuli. This could be linked to inappropriate modulation of attention leading to hyperimitation of actions. It has been observed that individuals with ASC require higher levels of perceptual load in order to ignore irrelevant distractors, and that the ASC participant’s performance (speed and accuracy) was not impaired with increasing perceptual load (Remington et al., 2009). This is in line with the idea that perceptual capacity is enhanced in ASC, as demonstrated by superior performance in visual search tasks (Riordan and Plaisted, 2001). It would therefore be interesting to examine whether participants with ASC performed similarly on the dual visual (oddball detection) task, as this might provide evidence for enhanced perceptual capacity in ASC relative to neurotypical participants. An fMRI study found that participants with ASC showed less neural activity than control participants in areas known to be active in response inhibition tasks (Kana et al., 2007). Moreover, in the more demanding inhibition task which involved working memory, they found that participants with ASC showed greater activation in premotor areas than control participants, suggesting inhibition circuitry is activated atypically in ASC, and further that inhibition might only be accomplished via strategic control as opposed to automatically in ASC. If this theory is correct then it is possible that ASC participants may have extra perceptual capacity to process the oddball movements in addition to the imitative compatibility task. If this were the case we might expect to see imitative compatibility effects even in a visual dual task scenario, or perhaps an over-spilling of resources (as in experiment 2) leading to enhanced imitative compatibility effects depending on the level of enhanced perceptual capacity available. This task could be developed further such that participants are required to actively ignore the movement of the stimuli. This would discriminate individuals with ASC are able to strategically control inhibition of irrelevant stimuli, the perception of which might not be typically suppressed (even in conditions of increased cognitive load).

Furthermore, a future study of therapeutic value would be to investigate whether people with ASC would show an increase in automatic imitation in the focused flash condition, and whether the carryover effect of seeing the smaller flash first that we have observed in experiment 7 would be present in a group of autistic participants. If so, this might suggest that attentional training to train individuals with ASC to pay attention to certain aspects of their social environment, e.g. to the eyes in order to read emotions, could be helpful in improving the quality of social interactions and increasing spontaneous imitation. If future interventions can enhance the ability to mimic facial expressions and emotions, then the fundamental impairment in social interaction in ASC may be greatly alleviated.

5.5.2 Future studies in neurotypical individuals

Future studies in neurotypical individuals could examine whether manipulating belief regarding the hand stimulus (i.e. informing participants it is an artificial computer-generated hand) would decrease or inhibit imitation. Although Liepelt and Brass (2010) found a reduction (as opposed to a complete inhibition) in imitative compatibility effects to be present in the ‘computer-generated/artificial’ condition, this may have been due to the fact that the stimulus used was less ambiguous (a gloved hand) and/or imitative compatibility may have been confounded with spatial compatibility in their experiment. These two possible interpretations could be teased apart using the current paradigm in experiment 9, where confounding spatial compatibility effects have been removed. Furthermore, due to the fact Liepelt and Brass (2010) used a between-subjects design, the differences in imitation in could potentially be explained by individual differences between groups, however the current paradigm uses a within-subjects design therefore removing this possibility.

Future studies could also examine whether some of the findings in the presented work do translate to real life mimicry. The results of experiments 1 and 2 support the idea that additional cognitive load in the same sensory modality inhibits imitation while cognitive load in a different sensory modality may facilitate imitation, relative to a baseline level of inhibition. In real life social interactions we are typically engaged in conversation, both speaking and listening. One possible implication for mimicry which could be drawn from the current results is that development of rapport and interest in a particular social interaction (i.e. vocal and auditory input) might contribute to facilitation of motor mimicry effects (in addition to social factors such as social attitudes which are known to increase imitation), due to the additional cognitive load occupying resources for active control of mimicry. On this basis, it would be interesting to examine whether interacting partners’ spontaneous motor mimicry of each other increases significantly in situations in which cognitive load is strained by another task relative to when cognitive load is not strained. Similarly, studies could examine whether real life spontaneous mimicry is inhibited in situations in which competing goal-relevant visual load is present. This could have implications for social interactions in populations with reduced cognitive capacity/inhibitory control.

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Appendix

Appendix A - Questionnaires

A1: The Edinburgh Laterality Inventory (for Handedness)

THE EDINBURGH LATERALITY INVENTORY (ELI)

SUBJECT CODE: **DATE:**

Indicate preferences in the use of the hands in the following activities by putting + in the appropriate column. Where the preference is so strong that the subject would never try to use the other hand unless absolutely forced to, put ++. If, in any case, the subject is really indifferent, put + in both columns.

Some of the activities require both hands. In these cases, the part of the task, or object, for which hand preference is wanted is indicated in brackets. Answer all of the questions, and only leave a blank if the subject has no experience at all of the object or task.

To calculate the Laterality Quotient (LQ), add the +s for each hand, subtract the sum for the left from that of the right, divide by the sum of both and multiply by 100. The LQ will range from -100 (absolutely L-handed) to +100 (absolutely R-handed)

Left		Right
	Writing	
	Drawing	
	Throwing	
	Scissors	
	Toothbrush	
	Knife (without fork)	
	Spoon	
	Broom (upper hand)	
	Striking match (match)	
	Opening box (lid)	

Appendix A2: Empathy Questionnaire EQ2 (Baron-Cohen and Wheelwright, 2004)

Questionnaire 2

Please fill in this information and then read the instructions below.

ALL INFORMATION REMAINS STRICTLY CONFIDENTIAL

Name:......................................

Today's date:.................................

<u>How to fill out the questionnaire</u>

Below are a list of statements. Please read each statement <u>very carefully</u> and rate how strongly you agree or disagree with it by circling your answer. There are no right or wrong answers, or trick questions.

IN ORDER FOR THE SCALE TO BE VALID, YOU MUST ANSWER EVERY QUESTION.

<u>Examples</u>

E1. I would be very upset if I couldn't listen to music every day.	strongly agree	[✓ slightly agree]	slightly disagree	strongly disagree
E2. I prefer to speak to my friends on the phone rather than write letters to them.	strongly agree	slightly agree	slightly disagree	[✓ strongly disagree]
E3. I have no desire to travel to different parts of the world.	[✓ strongly agree]	slightly agree	slightly disagree	strongly disagree
E4. I prefer to read than to dance.	strongly agree	slightly agree	[✓ slightly disagree]	strongly disagree

1. I can easily tell if someone else wants to enter a conversation.	strongly agree	slightly agree	slightly disagree	strongly disagree
2. I find it difficult to explain to others things that I understand easily, when they don't understand it first time.	strongly agree	slightly agree	slightly disagree	strongly disagree
3. I really enjoy caring for other people.	strongly agree	slightly agree	slightly disagree	strongly disagree
4. I find it hard to know what to do in a social situation.	strongly agree	slightly agree	slightly disagree	strongly disagree

5. People often tell me that I went too far in driving my point home in a discussion.	strongly agree	slightly agree	slightly disagree	strongly disagree
6. It doesn't bother me too much if I am late meeting a friend.	strongly agree	slightly agree	slightly disagree	strongly disagree
7. Friendships and relationships are just too difficult, so I tend not to bother with them.	strongly agree	slightly agree	slightly disagree	strongly disagree
8. I often find it difficult to judge if something is rude or polite.	strongly agree	slightly agree	slightly disagree	strongly disagree
9. In a conversation, I tend to focus on my own thoughts rather than on what my listener might be thinking.	strongly agree	slightly agree	slightly disagree	strongly disagree
10. When I was a child, I enjoyed cutting up worms to see what would happen.	strongly agree	slightly agree	slightly disagree	strongly disagree
11. I can pick up quickly if someone says one thing but means another.	strongly agree	slightly agree	slightly disagree	strongly disagree
12. It is hard for me to see why some things upset people so much.	strongly agree	slightly agree	slightly disagree	strongly disagree
13. I find it easy to put myself in somebody else's shoes.	strongly agree	slightly agree	slightly disagree	strongly disagree
14. I am good at predicting how someone will feel.	strongly agree	slightly agree	slightly disagree	strongly disagree

15. I am quick to spot when someone in a group is feeling awkward or uncomfortable.	strongly agree	slightly agree	slightly disagree	strongly disagree
16. If I say something that someone else is offended by, I think that that's their problem, not mine.	strongly agree	slightly agree	slightly disagree	strongly disagree
17. If anyone asked me if I liked their haircut, I would reply truthfully, even if I didn't like it.	strongly agree	slightly agree	slightly disagree	strongly disagree
18. I can't always see why someone should have felt offended by a remark.	strongly agree	slightly agree	slightly disagree	strongly disagree
19. Seeing people cry doesn't really upset me.	strongly agree	slightly agree	slightly disagree	strongly disagree
20. I am very blunt, which some people take to be rudeness, even though this is unintentional.	strongly agree	slightly agree	slightly disagree	strongly disagree
21. I don’t tend to find social situations confusing.	strongly agree	slightly agree	slightly disagree	strongly disagree
22. Other people tell me I am good at understanding how they are feeling and what they are thinking.	strongly agree	slightly agree	slightly disagree	strongly disagree
23. When I talk to people, I tend to talk about their experiences rather than my own.	strongly agree	slightly agree	slightly disagree	strongly disagree
24. It upsets me to see an animal in pain.	strongly agree	slightly agree	slightly disagree	strongly disagree
25. I am able to make decisions without being influenced by people's feelings.	strongly agree	slightly agree	slightly disagree	strongly disagree
26. I can easily tell if someone else is interested or bored with what I am saying.	strongly agree	slightly agree	slightly disagree	strongly disagree
27. I get upset if I see people suffering on news programmes.	strongly agree	slightly agree	slightly disagree	strongly disagree
28. Friends usually talk to me about their problems as they say that I am very understanding.	strongly agree	slightly agree	slightly disagree	strongly disagree
29. I can sense if I am intruding, even if the other person doesn't tell me.	strongly agree	slightly agree	slightly disagree	strongly disagree
30. People sometimes tell me that I have gone too far	strongly	slightly	slightly	strongly

with teasing.	agree	agree	disagree	disagree
31. Other people often say that I am insensitive, though I don’t always see why.	strongly agree	slightly agree	slightly disagree	strongly disagree
32. If I see a stranger in a group, I think that it is up to them to make an effort to join in.	strongly agree	slightly agree	slightly disagree	strongly disagree
33. I usually stay emotionally detached when watching a film.	strongly agree	slightly agree	slightly disagree	strongly disagree
34. I can tune into how someone else feels rapidly and intuitively.	strongly agree	slightly agree	slightly disagree	strongly disagree
35. I can easily work out what another person might want to talk about.	strongly agree	slightly agree	slightly disagree	strongly disagree
36. I can tell if someone is masking their true emotion.	strongly agree	slightly agree	slightly disagree	strongly disagree
37. I don't consciously work out the rules of social situations.	strongly agree	slightly agree	slightly disagree	strongly disagree
38. I am good at predicting what someone will do.	strongly agree	slightly agree	slightly disagree	strongly disagree
39. I tend to get emotionally involved with a friend's problems.	strongly agree	slightly agree	slightly disagree	strongly disagree
40. I can usually appreciate the other person's viewpoint, even if I don't agree with it.	strongly agree	slightly agree	slightly disagree	strongly disagree

Thank you for filling this questionnaire in.

Appendix A3: The autism spectrum quotient questionnaire (Baron-Cohen et al, 2001)

The Adult Autism Spectrum Quotient (AQ)

Name:..

Today's Date................................

How to fill out the questionnaire

Below are a list of statements. Please read each statement very carefully and rate how strongly you agree or disagree with it by circling your answer.

DO NOT MISS ANY STATEMENT OUT.

Examples

E1. I am willing to take risks.	definitely agree	slightly agree	[✓ slightly disagree]	definitely disagree
E2. I like playing board games.	definitely agree	[✓ slightly agree]	slightly disagree	definitely disagree
E3. I find learning to play musical instruments easy.	definitely agree	slightly agree	slightly disagree	[✓ definitely disagree]
E4. I am fascinated by other cultures.	[✓ definitely agree]	slightly agree	slightly disagree	definitely disagree

1. I prefer to do things with others rather than on my own.	definitely agree	slightly agree	slightly disagree	definitely disagree
2. I prefer to do things the same way over and over again.	definitely agree	slightly agree	slightly disagree	definitely disagree
3. If I try to imagine something, I find it very easy to create a picture in my mind.	definitely agree	slightly agree	slightly disagree	definitely disagree
4. I frequently get so strongly absorbed in one thing that I lose sight of other things.	definitely agree	slightly agree	slightly disagree	definitely disagree
5. I often notice small sounds when others do not.	definitely agree	slightly agree	slightly disagree	definitely disagree
6. I usually notice car number plates or similar strings of information.	definitely agree	slightly agree	slightly disagree	definitely disagree
7. Other people frequently tell me that what I’ve said is impolite, even though I think it is polite.	definitely agree	slightly agree	slightly disagree	definitely disagree
8. When I’m reading a story, I can easily imagine what the characters might look like.	definitely agree	slightly agree	slightly disagree	definitely disagree
9. I am fascinated by dates.	definitely agree	slightly agree	slightly disagree	definitely disagree
10. In a social group, I can easily keep track of several different people’s conversations.	definitely agree	slightly agree	slightly disagree	definitely disagree
11. I find social situations easy.	definitely agree	slightly agree	slightly disagree	definitely disagree
12. I tend to notice details that others do not.	definitely agree	slightly agree	slightly disagree	definitely disagree
13. I would rather go to a library than a party.	definitely agree	slightly agree	slightly disagree	definitely disagree
14. I find making up stories easy.	definitely agree	slightly agree	slightly disagree	definitely disagree
15. I find myself drawn more strongly to people than to things.	definitely agree	slightly agree	slightly disagree	definitely disagree
16. I tend to have very strong interests which I get upset about if I can’t pursue.	definitely agree	slightly agree	slightly disagree	definitely disagree
17. I enjoy social chit-chat.	definitely agree	slightly agree	slightly disagree	definitely disagree
18. When I talk, it isn’t always easy for others to get a word in edgeways.	definitely agree	slightly agree	slightly disagree	definitely disagree
19. I am fascinated by numbers.	definitely agree	slightly agree	slightly disagree	definitely disagree

20. When I'm reading a story, I find it difficult to work out the characters' intentions.	definitely agree	slightly agree	slightly disagree	definitely disagree
21. I don't particularly enjoy reading fiction.	definitely agree	slightly agree	slightly disagree	definitely disagree
22. I find it hard to make new friends.	definitely agree	slightly agree	slightly disagree	definitely disagree
23. I notice patterns in things all the time.	definitely agree	slightly agree	slightly disagree	definitely disagree
24. I would rather go to the theatre than a museum.	definitely agree	slightly agree	slightly disagree	definitely disagree
25. It does not upset me if my daily routine is disturbed.	definitely agree	slightly agree	slightly disagree	definitely disagree
26. I frequently find that I don't know how to keep a conversation going.	definitely agree	slightly agree	slightly disagree	definitely disagree
27. I find it easy to "read between the lines" when someone is talking to me.	definitely agree	slightly agree	slightly disagree	definitely disagree
28. I usually concentrate more on the whole picture, rather than the small details.	definitely agree	slightly agree	slightly disagree	definitely disagree
29. I am not very good at remembering phone numbers.	definitely agree	slightly agree	slightly disagree	definitely disagree
30. I don't usually notice small changes in a situation, or a person's appearance.	definitely agree	slightly agree	slightly disagree	definitely disagree
31. I know how to tell if someone listening to me is getting bored.	definitely agree	slightly agree	slightly disagree	definitely disagree
32. I find it easy to do more than one thing at once.	definitely agree	slightly agree	slightly disagree	definitely disagree
33. When I talk on the phone, I'm not sure when it's my turn to speak.	definitely agree	slightly agree	slightly disagree	definitely disagree
34. I enjoy doing things spontaneously.	definitely agree	slightly agree	slightly disagree	definitely disagree
35. I am often the last to understand the point of a joke.	definitely agree	slightly agree	slightly disagree	definitely disagree
36. I find it easy to work out what someone is thinking or feeling just by looking at their face.	definitely agree	slightly agree	slightly disagree	definitely disagree
37. If there is an interruption, I can switch back to what I was doing very quickly.	definitely agree	slightly agree	slightly disagree	definitely disagree
38. I am good at social chit-chat.	definitely agree	slightly agree	slightly disagree	definitely disagree
39. People often tell me that I keep going on and on	definitely	slightly	slightly	definitely

about the same thing.	agree	agree	disagree	disagree
40. When I was young, I used to enjoy playing games involving pretending with other children.	definitely agree	slightly agree	slightly disagree	definitely disagree
41. I like to collect information about categories of things (e.g. types of car, types of bird, types of train, types of plant, etc.).	definitely agree	slightly agree	slightly disagree	definitely disagree
42. I find it difficult to imagine what it would be like to be someone else.	definitely agree	slightly agree	slightly disagree	definitely disagree
43. I like to plan any activities I participate in carefully.	definitely agree	slightly agree	slightly disagree	definitely disagree
44. I enjoy social occasions.	definitely agree	slightly agree	slightly disagree	definitely disagree
45. I find it difficult to work out people's intentions.	definitely agree	slightly agree	slightly disagree	definitely disagree
46. New situations make me anxious.	definitely agree	slightly agree	slightly disagree	definitely disagree
47. I enjoy meeting new people.	definitely agree	slightly agree	slightly disagree	definitely disagree
48. I am a good diplomat.	definitely agree	slightly agree	slightly disagree	definitely disagree
49. I am not very good at remembering people's date of birth.	definitely agree	slightly agree	slightly disagree	definitely disagree
50. I find it very easy to play games with children that involve pretending.	definitely agree	slightly agree	slightly disagree	definitely disagree

Developed by:
The Autism Research Centre
University of Cambridge

Appendix A4: Questionnaire to measure how participants attended to and perceived differences between hand and block stimuli used in Experiment 1a and 1b, 2 and 3

Questionnaire

Please answer the following questions by drawing a single vertical line on the scale given to indicate your answer:

1. Watching the finger grabbed my attention more than watching the block.

Disagree Neither agree nor disagree Agree

2. Watching the block grabbed my attention more than watching the finger.

Disagree Neither agree nor disagree Agree

3. The clips of the block and finger were similar in terms of movement.

Disagree Neither agree nor disagree Agree

4. The clips of the block and the finger were similar in terms of appearance.

Disagree Neither agree nor disagree
Agree

5. Seeing the block move made me want to move my own finger.

Disagree Neither agree nor disagree
Agree

6. Seeing the finger move made me want to move my own finger.

Disagree Neither agree nor disagree

Agree

7. When watching each video clip, how much were you aware that you were seeing either the hand or block?

Not at all To some extent Very
much

1 2 3 4 5 6 7 8 9 10

8. When the video clips changed between the block and hand how much did you notice this change?

Not at all To some extent Very
much

1 2 3 4 5 6 7 8 9 10

9. To what extent, if at all, was watching the block move more interesting than watching the finger move?

Not at all To some extent Very
much

1 2 3 4 5 6 7 8 9 10

10. To what extent, if at all, was watching the finger move more interesting than watching the block move?

Not at all To some extent Very much

1 2 3 4 5 6 7 8 9 10

Appendix A5: **‘**Belief’ questionnaire (Experiment 5 and 6)

End of Experiment Questionnaire

1. When you saw the block for the **second time**, did you think of the object as more of a ‘block representation’ of the hand, ***compared to*** when you had seen the block for the first time?

Not at all To some extent Very
much

2. When you saw the block for the second time, to what extent did you think of the block as a hand ***compared to*** when you had seen the block for the first time?

Not at all To some extent Very much

3. When you saw the block for the **second time**, to what extent do you think that knowing that it represented a hand influenced your perception of the block movement, making the block seem to move in a more hand-like way, ***compared to*** when you saw the object the first time?

Not at all To some extent Very
much

4. When you were told the block represented a hand movement, how much did you **believe** that this was true?

Not at all To some extent Very much

5. When you were told the block represented a hand movement, how much did you **think about** this during the second half of the experiment?

Not at all To some extent Very much

Appendix A6: Experiment 7 questionnaire regarding attention to stimulus movement in diffuse vs focused flash conditions. Questionnaire 1 was completed twice: after the focused flash and diffuse flash sections of the experiment.

<u>Questionnaire 1</u>

Please indicate your answer using a vertical line anywhere on the scale

1. How much attention were you paying to the moving index finger?

No attention Some attention All of my attention

2. How much attention were you paying to the fist of the hand (the rest of the hand excluding the moving index finger)?

No attention Some attention All of my attention

3. How much attention were you paying to areas of the screen outside of the image of the hand and moving finger?

No attention Some attention All of my attention

4. How much attention were you paying to the direction of the movement of the finger (up or down)?

No attention Some attention All of my attention

5. How much did you feel that the movement of the finger made you want to move your own finger?

Not at all To some extent Very much

End of Experiment Questionnaire

1. Do you think you paid more or less attention to the movement of the finger when the flash was constricted to the area with the small flash?

Less No difference More

2. Please indicate (circle) which flash you feel was more successful in focusing your attention on the **movement of the finger**:

a) the small flash

b) the large flash

c) no difference

Appendix A7: 'Belief' questionnaire (Experiment 8 and 9)

Questionnaire – Part 1

1. During the first half of the experiment, did you at any time think that the moving rectangle might represent a human finger movement?

Not at all To some extent Very much

1 2 3 4 5 6 7 8 9 10

2. To what extent, if at all did the movement of the rectangle remind you of a human finger movement?

Not at all To some extent Very much

1 2 3 4 5 6 7 8 9 10

3. Seeing the rectangle move made me want to move my own finger

Disagree Neither agree nor disagree Agree

1 2 3 4 5 6 7 8 9 10

End of Experiment Questionnaire

1. When you saw the rectangle for the second time, did you think of the rectangle as more of a 'block representation' of a moving finger, compared to when you had seen the rectangle for the first time?

Not at all To some extent Very much

1 2 3 4 5 6 7 8 9 10

2. When you saw the rectangle for the second time, to what extent did you think of the moving rectangle as being a human finger compared to when you had seen the block for the first time?

Not at all To some extent Very much

3. To what extent do you think that knowing that it represented a moving finger of a human hand influenced your perception of the movement, making the rectangle seem to move in a more human way, compared to when you saw the object the first time?

Not at all To some extent Very much

4. Seeing the rectangle move, in the knowledge that the movement represented a human finger movement, made me want to move my own finger.

Disagree Neither agree nor disagree Agree

5. When you were told the rectangle represented a finger movement, how much did you **believe** that this was true?

Not at all To some extent Very much

6. When you were told the rectangle represented a finger movement, how much did you **think about** this during the second half of the experiment?

Not at all To some extent Very much

Appendix B - Significant main effects and interactions that were not directly relevant to the experimental hypotheses

Appendix B1: Experiment 1a

There was a significant main effect of SOA (*F*(2,38) = 88.561, *p* = .000), indicating that mean RTs were significantly slower at an SOA of 0ms than at 120ms and 280ms. This finding reflects typical temporal expectancy in RT tasks using a number of time points (Niemi and Näätänen, 1981). The longer the period of time between presentation of the stimulus and the appearance of the go signal, the higher the probability of the go signal appearing; thus expectancy of the go signal increases leading to faster RTs. The main effect of stimulus was approaching significance (*F*(1,19) = 3.918; *p* = .062), indicating that mean RTs for the finger stimulus (M = 321.50ms) were faster than RTs for the object stimulus (M = 325.54ms).

There was also an interaction between stimulus and SOA which was bordering on significance (*F*(2,28) = 3.151, *p* = .054), indicating that there was a significant difference between the difference in RTs between the finger and object stimulus at 0ms (M = -9.56ms) compared to 280ms (M = 1.13ms) (*t(*19) = -1.365, *p* = .029). The difference between the difference in RTs for the finger and object stimulus at 120ms (M = -3.69ms) compared to 280ms (M = 1.13ms) was approaching significance (*t*(19) = -1.951, *p* = .066). However, there was no significant difference between the difference in RTs for the finger and object stimulus between 0ms and 120ms (*t*(19) = -1.109, *p* = .281). Paired t-tests also revealed that RTs were significantly faster for the finger stimulus (M = 356.42ms) compared to the object stimulus (M = 365.98ms) at 0ms SOA (*t(*19) = -2.185, *p* = .042), however there was no significant difference between RTs for the finger and object at 120ms or 280ms (*p* >.109).

Appendix B2: Experiment 1b

There was a significant main effect of SOA (*F*(2,38) = 58.720, *p* = .000) indicating that, as in experiment 1a, participants RTs were significantly faster in response to an SOA of 120ms and 280ms compared to an SOA of 0ms.

Appendix B3: Experiment 5

There was the usual significant main effect of SOA (*F* (2,44) = 72.984, *p* = .000). There was also a significant main effect of condition (*F* (2,66) = 2.781, *p* = .048) and a significant interaction between condition and SOA (*F*(6,132) = 2.241, *p* = .043), indicating that: 1) the difference in RTs between the object (section 3) and the finger conditions was greater at 0ms (M = -16.05ms) compared to 120ms (M = -3.56ms) (*t*(22) = -2.832, *p* = .010); 2) the difference in RTs between the object (section 3) and the finger condition was greater at 280ms (M = -15.17ms) compared to 120ms (M = -3.56ms) (*t*(22) = 2.3832, *p* =.026); 3) the difference in RTs between the object (section 1) and the finger condition was greater at 280ms (M = -7.10ms) compared to 120ms (M = 2.54ms) (t(22) = 2.732, p = .012); 4) the difference in RTs between the object (section 3) and the finger condition was greater at 0ms (M = -8.41ms) compared to 120ms (5.39ms) (*t*(22) = -2.258, *p* = .034); 5) the difference in RTs between the finger and belief condition was greater at 280ms (M = 17.34ms) compared to 120ms (M = 7.27ms) (*t*(22) = -2.07, *p* = .016). In addition, the difference in RTs between the object (section 3) and belief condition was greater at 120ms (M = 11.49ms) compared to 0ms (M = 2.89ms) and this difference was approaching significance (*t*(22) = -1.892, *p* =.072). Paired t-tests also revealed that RTs were: 1) significantly faster for the object condition (section 3) (M = 289.12ms) compared to the finger condition (304.29ms) at 0ms (*t*(22) = -2.658 , *p* = .014); 2) faster for the object condition (Section 3) (289.12ms) compared to the finger condition (304.29ms) (*t*(22) = -4.185, *p* = .000) at 280ms and 3) faster the belief condition (287.49ms) compared to the finger condition (304.29ms) at 280ms (*t*(22) = 2.960, *p* = .007) **(Figure 45)**. No other main effects or interactions were significant (p>.245).

Appendix B4: Experiment 6

This revealed the usual significant main effect of SOA (*F*(2,58) = 68.654, *p* = .000) and a significant main effect of condition (*F*(1,29) = 17.621, *p* = .000) indicating that RTs were significantly faster in the ‘before belief’ condition (284.56ms) and were significantly slower in the ‘after belief’ condition (306.84ms).

Finally, there was a significant interaction between condition and SOA (*F*(2,58) = 24.343, *p* = .000), indicating that the difference in RTs for the object and belief conditions was significantly greater at 0ms (M= -44.54ms) compared to 120ms (M = -10.66ms), and was also greater at 0ms (M= -44.54ms) compared to 280ms (M = -11.64ms). However there was no significant difference between the difference in RTs for the object and belief conditions at 120ms (M = -10.66ms) compared to 280ms (M = -11.64ms). Paired t-tests also revealed that participants’ RTs were significantly faster in the object condition at all three time points (0ms SOA – 298.48ms; 120ms SOA– 286.30ms; 280ms SOA – 268.91ms) relative to the belief condition (0ms SOA – 343.01ms; 120ms SOA – 296.96; 280ms SOA – 280.55ms); however the size of this effect was greatest at 0ms SOA (*t*(29) = -5.291, *p* = .000), followed by 280ms (*t(*29) = -2.391, *p* = .024) and 120ms (*t*(29) = -2.355, *p* = .025) **(Figure 50).** No other main effects or interactions were significant (p>.138).

Appendix B5: Experiment 8

For pressing responses there was a main effect of compatibility (F(1,18) = 13.849, p = .002). There was a significant interaction between condition and SOA (F(2,72) = 2.918, p = .027) indicating that: 1) the difference in RTs for the object and belief conditions was significantly different at 0ms (M = -7.38) compared to 120ms (M = 8.88ms) (*t*(18) = -2.283, *p*

= .035).; 2) the difference in RTs for the object and belief conditions was significantly different at 0ms (M = -7.38) compared to 280ms (12.87ms) (t(18) = -2.757, p = .013); 3) the difference in RTs for the belief and finger condition was significantly different between 0ms (M = 5.91ms) and 280ms (M = -14.75ms) (*t*(18) = 2.629, *p* = .017); 4) the difference in RTs for the belief and finger condition was significantly different between 120ms (M = 2.04ms) and 280ms (M = -14.75ms) (t(18) = 2.178, p = .043). Paired t-tests also revealed that RTs were significantly faster in the belief condition (M = 297.97ms) compared to the object condition at 280ms (t(18) = 2.393, p = .028).

For releasing responses, there was an interaction between condition and SOA (F(4,72) = 7.969, p = .000) indicating that: 1) the difference in RTs for the object and belief conditions was significantly different at 120ms (M= 10.06ms) compared to 0m (M = -10.90ms) (*t*(18) = -3.561, *p* = .002), and significantly different at 280ms (M = 4.79ms) compared to 0ms (M = -10.0ms) (*t*(18) = -2.191, *p* = .042); 3) the difference in RTs for the belief and finger conditions was significantly different at 120ms (-10.1ms) compared to 0ms (7.27ms), and significantly different at 120ms (13.95ms) compared 280ms (-10.16ms); 4) the difference in RTs for the object and finger conditions was significantly different at 120ms (24.01ms) compared to 0ms (-3.3ms) , and was significantly different at 120ms (24.01ms) compared to 280ms (-5.37ms). Paired t-tests also revealed that RTs were significantly faster for the hand condition (294.74ms) compared to the object condition (318.75ms) at 120ms (*t*(18) = 3.197, *p* =.005), and were significantly faster for the hand condition (294.74ms) compared to the belief condition (308.69ms) (*t*(18) = 2.375, *p* = .029).

Appendix B6: Experiment 9

For the Thumb down condition, there was the usual main effect of SOA (*F*(2,34) = 74.508, *p* = .000).There was a main effect of condition (*F*(2,34) = 4.418, *p* = .020). There was also a significant interaction between condition and SOA (*F*(4,72) = 2.919, *p* = .027) indicating that the difference in RTs for the object and belief conditions was significantly different at 0ms (M = -36.76ms) compared to120ms(M = -19.55ms) (t(17) = -4.086, p = .001), and 0ms (M = -36.76ms) compared to 280ms (M = -16.03ms) (t(17) = -3.073, p = .007). In addition, the difference in RTs for the object and hand conditions was significantly different ay 0ms (M = -18.19ms) compared to 120ms (M = -5.67ms) (t(17) = -2.644, p = .017). The remaining comparisons between condition and SOA did not reach statistical significance (*p* > .141). Paired t-tests also revealed that RTs for the object condition were faster (M =349.10ms) compared to the belief condition (M =385.86ms) at 0ms (*t*(17) = - 3.116, *p* = .006); 2) RTs were faster for the hand condition (M =385.86ms) compared to the belief condition (M =367.29ms) at 0ms (*t*(17) = 2.153, *p* = .046); 3) RTs were significantly faster for the object condition (M =349.10ms) compared to the hand condition (M =367.29ms) at 0ms (*t*(17) = -2.640, *p* = .017).

For the Thumb up condition, there was the usual main effect of SOA (*F*(2,34) = 51.026, *p* = .000). There was a main effect of condition was approaching significance (*F*(2,34) = 3.103, *p* = .058). There was a significant interaction between condition and SOA (*F(*4,72) = 2.850, *p* =.049) indicating that: 1)the difference in RTs for the object and belief conditions was significantly different at 0ms (M = -37.73ms) compared to120ms(M = -17.59ms) (t(17) = -2.241, p = .041), and 0ms (M = -37.73ms) compared to 280ms (M = -17.59ms) (t(17) = -2.248, p = .038). In addition, the difference in RTs for the object and hand conditions was significantly different ay 0ms (M = -23.60ms) compared to 120ms (M = .71ms) (*t*(17) = -3.210, *p* = .005).The remaining comparisons between condition and SOA did not reach statistical significance (*p* > .079).Paired t-tests also revealed RTs were significantly faster for the object condition (M = 234.94ms) compared to the belief condition (M =390.14ms) at 0ms SOA (*t*(17) = -9.102, *p* = .000) and RTs were significantly faster for the object condition (M =234.94ms) compared to the hand condition (M =376.00ms) at 0ms SOA (*t*(17)= 12.824, *p* = .000). The remaining comparisons between SOA and condition did not reach statistical significance (*p* > .078).

Appendix C – Changes to stimuli

Appendix C1: Colour and luminance in each experiment. Luminance was measured using a Chroma Meter CS-100.

Experiment	Colour of object stimulus image	Stimulus Maximum Luminance readings
1(a-b), 2, 4 and 3	Pale pink/beige	Object – 95.5 Finger min – 28.5 Finger max– 142
5 and 6 + 7 (finger only)	Pale pink	Object – 141 Finger min – 28.5 Finger max– 142
8 and 9	Blue	Object - 142 Finger min – 28.5 Finger max– 142

Appendix C2: Changes made to stimulus images throughout thesis

Chapter 2

Experiments 1-3

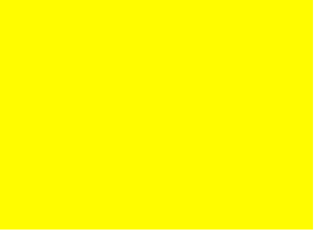
Hand (mirror view)

Object (mirror view)

Hand (anatomical view)

Object (anatomical view)

Experiments 1-3: Diffuse flash go signal



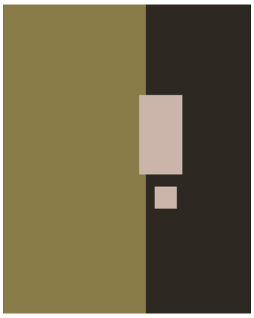
Chapter 3 and 4

Experiments 4, 5, 6, 7 + 8

Rotated hand

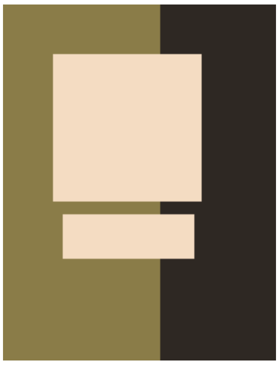
Experiment 4

Rotated object



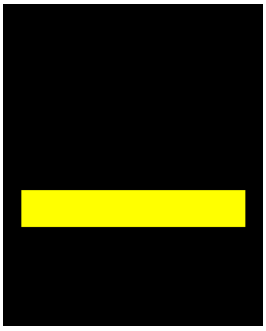
Experiments 5 + 6

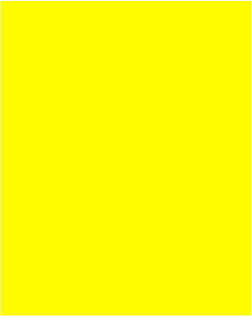
Rotated object (size and brightness increased)



Experiments 4-6: Diffuse flash go signal

Experiment 7: Both diffuse and focused flash go signal (comparison)





Experiment 8

Rotated object (single pale blue object)

Experiment 9

Object (thumb down)

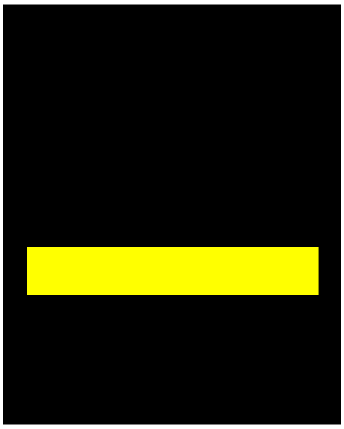
Object (thumb up)

Hand (thumb down)

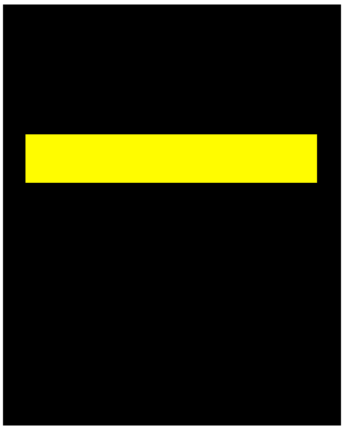
Hand (thumb up)

Experiments 8 + 9 focused go signal:

Experiment 8 and 9 (thumb down)



Experiment 9 (thumb up)



Appendix C3: Summary of the key features of the experiments presented in this thesis

Ch.	**Expt.**	**Stimuli used**	**Stimulus Presentation**	**Go signal used**	**Short summary of changes made**
2	**1a and 1b**	Hand stimulus and object stimulus comprised of large stationary rectangle and small moving square (as in Gowen et al 2010)	Mixed On Laptop	Diffuse	Stimuli presented from mirror and anatomical view In experiment 1b, a secondary visual oddball detection task was used, while only the imitation task was performed in experiment 1a
2	**2**	Stimuli were identical to experiment 1a and 1b	Mixed Laptop	Diffuse	Stimuli presented from mirror and anatomical view Secondary auditory task was used
2	**3**	Stimuli were identical to experiment 1a and 1b	Blocked Laptop	Diffuse	Stimuli presented from mirror and anatomical view
3	**4**	Stimuli were identical to experiment 1a and 1b	Blocked Laptop	Diffuse	Stimuli were rotated to create a neater version of the paradigm, removing the need for two views
3	**5**	The size, dimensions, colour and luminance of the object stimulus was altered (see **Appendix**) to more closely resemble the hand stimulus and consisted of a larger stationary square and a larger moving rectangle	Blocked Computer	Diffuse	Rotated stimuli were used Participants belief regarding the agency of the object stimulus was manipulated Experiment consisted of 4 parts: 1) Object; 2) hand; 3) object; 4) belief (object)
3	**6**	Object stimulus only (object stimulus was identical to that presented in experiment 5)	Blocked Computer	Diffuse	Rotated stimuli were used Participants belief regarding the agency of the object stimulus was manipulated Experiment consisted of 2 parts: 1) object; 2) belief (object); and the hand stimulus was not presented
4	**7**	Hand stimulus only	Blocked Computer	Diffuse & Focused	Rotated stimuli were used A new flash designed to focus attention on stimulus movement was compared with the previous diffuse yellow flash Eye-tracking was conducted
4	**8**	Hand and object stimuli used The object stimulus was altered to consist of a single pale blue horizontally set rectangle	Blocked Computer	Focused	Rotated stimuli were used Participants belief regarding the agency of the object stimulus was manipulated Experiment consisted of 3 parts: 1) object; 2) belief (object); 3) Hand
4	**9**	Stimuli were identical to experiment 8	Blocked Computer	Focused	Rotation of stimuli was altered to remove confounding Simon effect, isolating the imitative component; stimuli were presented in two rotated orientations Participants belief regarding the agency of the object stimulus was manipulated Experiment consisted of 3 parts: 1) object; 2) belief (object); 3) Hand