Automatic imitation and associative learning

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Abstract

Human body movements are especially effective in eliciting imitative responses. This thesis aims to establish why this is the case, and fundamentally, what this suggests about the mechanisms mediating imitation. Chapter 1 outlines theories which can account for this imitative bias, and highlights issues upon which these theories can be distinguished.

Chapter 2 establishes whether the finding that responses are executed faster in response to stimuli of the same action type reflects an automatic tendency to imitate observed actions. On the basis of evidence to support this hypothesis, Chapters 3 and 4 use this reaction time measure to investigate imitation mechanisms.

Chapter 3 addresses whether the human imitative bias emerges through top-down modulation of imitation mechanisms, on the basis of knowledge about whether stimuli are of human origin, or through perceptual properties of stimuli. These experiments suggest that automatic imitation effects are larger with human stimuli than robotic stimuli, but are unaffected by beliefs about stimulus identity, indicating that the imitative bias is driven by perceptual properties of stimuli.

Chapter 4 asks why the perceptual properties of human stimuli are especially effective in eliciting imitative responses. On the basis of evidence suggesting that training can modulate imitation of robotic stimuli, this chapter supports the hypothesis that the imitative bias results from greater opportunity for associative learning with human stimuli.

Chapter 5 investigates whether visuotactile integration can be modulated through training, in a similar way to visuomotor integration. By recording event-related brain potentials in response to tactile stimulation following visuotactile training, Chapter 5 indicates that visuotactile integration is modulated following training, but there are some differences in the influences of training with human and non-human visual stimuli.

In summary, the results of the experiments reported in this thesis support the hypothesis that the human imitative bias emerges because of perceptual properties of human stimuli and greater opportunity to form associations between these stimuli and matching responses. These findings are consistent with the Associative Sequence Learning model of imitation. Visuotactile integration may also be understood with reference to associative learning.

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I, Clare Press, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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Chapter 1: Introduction

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1.1 Introduction

A common reaction to observing someone wave is to wave back. The action which is executed is said to match the action which is observed because it is visually similar from a third party perspective. Imitation is the term used to refer to behaviour of this type which matches a previously observed action, and which is causally related to having observed that action.

Many processes are required for effective imitation, including vision, motor control and working memory. However, the process which distinguishes imitation from other action and perception is translation of the visual representation of an action into a matching motor representation. The visual representation of action enters the brain as a retinal pattern of stimulation, and this representation must be translated into motor commands which will produce that retinal pattern of stimulation from a third party perspective. Patterns of stimulation on the retina and muscle commands would appear to be in incommensurable codes, therefore effective imitation requires resolution of the 'correspondence problem' (e.g. Alissandrakis, Nehaniv, & Dautenhahn, 2002). This problem is especially evident for perceptually opaque actions (Heyes & Ray, 2000), that is, those actions where the visual feedback generated when executing the action oneself differs from the visual feedback generated when observing another individual executing that action. For example, when observing someone else touching their ear, the hand can be seen moving upwards towards the ear until it makes contact. In contrast, when touching ones own ear, in many postures the visual feedback generated is non-existent. Understanding imitation and supporting mechanisms therefore importantly requires addressing how the correspondence problem is solved.

This chapter will begin in section 1.2 by considering various types of research into imitation, and the specific methods which are appropriate for investigation of how we solve the correspondence problem. It will examine two theories which address the correspondence problem, with evidence currently distinguishing these theories. Section 1.3 introduces the specific issue under investigation in this thesis, namely why human actions may be especially effective in eliciting imitative responses. Several hypotheses will be proposed, along with consideration of the questions which will be addressed in order to distinguish these hypotheses in empirical chapters 2 to 4. Section 1.5 summarises the research and hypotheses under investigation in this thesis, along with ways in which they will be tested in subsequent empirical chapters.

1.2 Imitation

Imitative behaviour is investigated by many researchers with different purposes. For example, comparative psychologists are pre-occupied with whether animals are capable of imitation (e.g. Voelkl & Huber, 2000; Custance, Whiten, & Bard, 1995). Developmental psychologists investigate the age at which children begin to imitate (e.g. Meltzoff & Moore, 1977), whether certain forms of imitation indicate understanding of goals in children (e.g. Bekkering, Wohlschläger, & Gattis, 2000), and whether imitative abilities in early life predict other sociocognitive abilities later in life (e.g. Charman, 2003; Charman et al., 2003; Charman & Baird, 2002). Those investigating 'observational learning' address whether observing another performing an action can accelerate learning of that action (e.g. Bird & Heyes, 2005; Kelly & Burton, 2001) and those investigating links between imitation and empathy have examined whether imitative behaviour differs between more and less empathic individuals (e.g. Chartrand & Bargh, 1999).

Investigating mechanisms responsible for solving the correspondence problem may be informed through use of automatic imitation paradigms. Automatic imitation refers to the finding that participants are faster, or more likely, to perform responses which match observed actions, than to perform responses which do not match, even if they are not explicitly instructed to imitate or are even given alternative tasks. Research into intentional imitation must necessarily address social processes which may influence the motivation of observers to imitate, in addition to mechanisms which solve the correspondence problem. Investigating imitation which occurs when the participant is not intentionally copying an action can decrease the influence of these social processes. Given that this thesis is concerned with investigating mechanisms which solve the correspondence problem, this review and subsequent empirical chapters will focus on automatic imitation.

Section 1.2.1 will review recent evidence of automatic imitation and section 1.2.2 will address possible neurological substrates. Section 1.2.3 will consider theories of imitation which address the correspondence problem, and section 1.2.4 will examine evidence currently distinguishing these theories.

1.2.1 Behavioural studies

Recent research suggests that observing an action automatically activates motor representations of that action, even without the intention to imitate. For example, Chartrand & Bargh (1999) found that when participants interacted with a confederate who was consistently rubbing his face or shaking his foot, the participants were more likely to rub their own face or shake their own foot, respectively. However, when asked if the confederates displayed any particular mannerisms, participants seemed unaware of these gestures.

Dimberg, Thunberg, & Elmehed (2000) similarly found some evidence of automatic imitation, using a priming paradigm where emotional face stimuli were imitated but did not appear to be consciously perceived. Happy, angry or neutral faces were presented for 30ms, directly followed by a neutral face mask. Despite self-report measures suggesting that participants did not consciously perceive these stimuli, muscles around the mouth were more active when observing happy, rather than angry, face primes, and muscles around the brow were more active when observing angry, rather than happy, face primes.

However, participants in the studies of Chartrand & Bargh (1999) and Dimberg et al. (2000) may have understood that their task required imitation even if, during post-test questioning, there was no conscious recall of the stimuli presented. Post-test questioning is not an ideal measure of conscious perception of stimuli (Shanks & St.John, 1994), and although participants were not explicitly instructed to imitate observed actions, there was no explicitly defined task. With no explicitly defined task, participants may have formulated their own task to imitate observed stimuli.

Stimulus-response compatibility procedures may be better suited to investigation of automatic imitation than the procedures employed by Chartrand & Bargh (1999) and Dimberg et al. (2000), because there is an explicitly defined task. Brass, Bekkering, & Prinz (2001) conducted a simple reaction time (RT) study requiring participants to execute a pre-specified action (move their index finger up or down) as soon as they detected an index finger begin to move up or down in the observed video display. The observed action therefore indicated to participants at what time they should respond, but not which response was appropriate. The authors found a compatibility effect such that pre-specified actions (e.g. moving their index finger upwards) were executed faster in response to observation of compatible (upwards), rather than incompatible (downwards), finger actions. Heyes, Bird, Johnson, & Haggard (2005) found a similar compatibility effect with opening and closing hand actions. Such stimulus-response compatibility paradigms are thought to indicate automatic imitation because the intention of participants is to perform an action of a certain type regardless of the observed action type, but despite this intention, participants are faster to imitate than to counter-imitate observed actions.

Kerzel & Bekkering (2000) observed a similar automatic imitation effect in a choice RT procedure when the response had not been prepared in advance. Participants reading words printed on a computer screen (e.g. ‘ba’), responded faster if a model behind these words was also mouthing the same word (‘ba’), rather than a different word (‘da’). In a similar procedure, Stürmer, Aschersleben, & Prinz (2000) required participants to observe the fingers of a human hand either spreading apart (opening) or grasping (closing), and were required to execute one of these two actions whenever they detected the stimulus hand change colour (e.g. close their hand when the hand turned blue and open their hand when it turned red). When the task-irrelevant stimulus action type (e.g. opening) was the same as that which should be executed (opening), responses were faster than if the task-irrelevant stimulus action type was different to that which should be executed (closing).

Stürmer et al. (2000) showed that terminal postures are as effective as moving action stimuli in eliciting automatic imitation; stills of fully closed and opened hand stimuli evoked imitation effects which were equivalent to those elicited by closing and opening hand movements. Craighero, Bello, Fadiga, & Rizzolatti (2002) and Vogt, Taylor, & Hopkins (2003) obtained similar evidence of automatic imitation with stimulus pictures of hands grasping bars at one of two orientations.

1.2.2 Neurological evidence

In the last ten years, many studies using electrophysiological and imaging techniques have found that areas of the cortex which are activated when executing actions are also activated when observing actions. These cortical areas reveal candidate neural mechanisms of imitation. Although this thesis is not primarily concerned with the neural mechanisms of imitation, the studies investigating these mechanisms can often contribute to the understanding of the corresponding psychological processes. The following section will examine the evidence relating to these candidate neural mechanisms of imitation.

The most widely-cited evidence of cortical areas involved when both observing and executing action comes from research investigating 'mirror neurons' in the monkey premotor cortex (Ferrari, Maiolini, Addessi, Fogassi, & Visalberghi, 2005; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Keysers et al., 2003; Kohler et al., 2002; Umilta et al., 2001; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992) and parietal lobule (Fogassi et al., 2005; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002; Fogassi, Gallese, Fadiga, & Rizzolatti, 1998). These neurons have been found to fire both when the monkey performs an action and when it observes the experimenter performing the same action. For example, a neuron may fire when the monkey executes a precision grip and also when it observes the experimenter executing a precision grip.

Various methodologies suggest that there are also areas in the human cortex which are activated when both observing and executing action. These areas are thought to be homologous to those in which mirror neurons have been found in the monkey. For example, using functional magnetic resonance imaging (fMRI), Iacoboni et al. (1999) found that both observing and executing finger actions activated the left premotor cortex and right superior parietal lobule. Other fMRI and positron emission tomography (PET) studies have found premotor and parietal activation when observing hands grasping objects (Grezes, Armony, Rowe, & Passingham, 2003; Hamzei et al., 2003), hands manipulating objects (Chaminade, Meltzoff, & Decety, 2002; Decety, Chaminade, Grezes, & Meltzoff, 2002), pantomimes of hand actions with objects (Grezes, Costes, & Decety, 1999; Grezes, Costes, & Decety, 1998; Decety et al., 1997) and speech-related and biting actions (Buccino et al., 2004). Electroencephalography (EEG) and magnetoencephalography (MEG) methods also provide converging evidence that motor processes operate when observing hand actions (Muthukumaraswamy & Johnson, 2004; Babiloni et al., 2002; Nishitani & Hari, 2000; Cochin, Barthelemy, Roux, & Martineu, 1999; Hari et al., 1998), facial expressions (Nishitani & Hari, 2002) and whole body movements (Cochin, Barthelemy, Lejeune, Roux, & Martineau, 1998).

Buccino et al. (2001) found evidence in an fMRI study that premotor activation may be action specific, finding that mouth, hand and foot action observation activate the premotor cortex somatotopically. The somatotopy was congruent with the motor organisation of the region (Penfield & Rasmussen, 1952), that is, the activation was most ventral for mouth actions and most dorsal for foot actions. Wheaton, Thompson, Syngeniotis, Abbott, & Puce (2004) likewise found somatotopic organisation in premotor and parietal cortex when observing face, hand and leg actions.

However, imaging studies can only demonstrate that overlapping brain regions are activated when observing and executing certain actions. Observing and executing actions could activate different neuronal populations, not distinguished with fMRI and PET resolution. Transcranial magnetic stimulation (TMS) provides more reliable evidence of the similarity of motor areas activated when observing and executing action. Fadiga, Fogassi, Pavesi, & Rizzolatti (1995) delivered TMS over the motor cortex while participants observed an experimenter performing actions. TMS-induced motor-evoked potentials (MEPs) in the hand muscles were larger when participants observed hand actions which would rely upon these muscles rather than arm actions which would not rely upon these muscles. In contrast, MEPs in the arm muscles were equal when participants observed hand and arm actions, which would both rely upon these muscles. Other studies have similarly found that TMS-induced MEPs are facilitated only, or to a greater extent, in the muscles being used in the observed actions (Watkins, Strafella, & Paus, 2003; Aziz-Zadeh, Maeda, Zaidel, Mazziota, & Iacoboni, 2002; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Strafella & Paus, 2000). In addition, Gangitano, Mottaghy, & Pascual-Leone (2001; 2004) provide converging evidence of the specificity of evoked motor representations, finding that MEPs reflect the time course of the observed action. When performing a grasping action, activation of the first dorsal interosseus muscle in the index finger increases as the distance between the fingers becomes greater. Gangitano and colleagues found that this temporal pattern was also observed when participants observed grasping actions.

The studies described in this section therefore suggest that some cortical areas are implicated both when executing and observing action. These areas are candidate neural mechanisms of imitation.

1.2.3 Theories of imitation

Sections 1.2.1 and 1.2.2 have surveyed evidence that humans are able to solve the correspondence problem, and that we can do so automatically; observing an action appears to automatically activate motor representations of that action. However, the surveyed studies do not directly address the correspondence problem, that is, they do not explain how we acquire the information concerning which motor representations of action correspond to which visual representations. The following section will consider two theories of imitation which address the correspondence problem.

Meltzoff & Moore's Active Intermodal Mapping (AIM) theory of imitation (e.g. Rao, Shon, & Meltzoff, in press; Meltzoff & Decety, 2003; Meltzoff & Moore, 1997) was developed in order to explain their finding that newborn infants can imitate facial gestures. Meltzoff & Moore hypothesise that there is an innate module for imitation, and that this module contains supramodal representations of the locations of body parts in relation to one another ('organ relations'). Once infants are able to move, they can learn the relationship between these organ relations and the motor commands which achieve them. Given that organ relations are specified supramodally, moving *in utero* can even allow infants to learn these relationships before they are born, through proprioceptive activation of organ relations. Innate supramodal representation of organ relations and opportunity for moving *in utero* will allow a newborn to imitate because an observed action will be converted into organ relations, and the infant has learnt how to achieve these organ relations with his own actions.

Although the AIM model is formulated to explain infant imitation, Meltzoff & Moore (1997) consider adult imitation to be performed via a similar mechanism. They suggest that the only major developmental change, which may occur within the first few weeks of life, is that the means of achieving an observed organ relation will be matched in addition to the organ relation itself. This transition is possible because of learnt relationships between organ relations and the actions which achieve them.

Meltzoff & Moore therefore consider that the correspondence problem is solved through innate specification of supramodal representations of organ relations. However, the AIM model is currently underspecified concerning what precisely is represented in these supramodal codes. This underspecification leads to some incomplete logic within the model. For example, Meltzoff & Moore do not specify why viewed actions are automatically represented as supramodal organ relations. It is therefore unclear how learning the relationship between organ relations and the movements which achieve these organ relations can lead to effective *imitation* of the precise movements which achieve organ relations; there is no reason to assume that such learning can allow *visual* representations of action to be encoded in terms of precise movements instead of organ relations.

In contrast to the AIM model, the Associative Sequence Learning (ASL) model of imitation (Brass & Heyes, 2005; Heyes, 2003; Heyes, 2001; Heyes & Ray, 2000) proposes that the ability to imitate is not innate, but develops through learning bidirectional 'vertical' associations between visual and motor representations of action. These associations can form whenever opportunities are presented for associative learning. For the purposes of this thesis, it will be considered that an opportunity for associative learning is present whenever there is temporal contiguity between two events (Hebb, 1949), and also contingency, that is, a predictive relationship between two events (e.g. Kamin, 1969; Rescorla, 1968).

Opportunities to associate visual and motor representations of the same action are abundant during development. For 'perceptually-transparent' actions such as hand and arm actions, the opportunities for associative learning can be provided through self-observation. For example, if observing ones hand opening whilst simultaneously executing the motor commands to open ones hand, the visual and motor representations of an opening hand may become associated. For 'perceptually-opaque' actions, such as face and whole body actions, the visual input received upon execution differs from that received upon observation of another performing that action. However, the environment still provides plenty of opportunities for relevant associative learning with perceptually-opaque actions. First, within our environment are many reflective surfaces and mirrors, allowing indirect observation of action. Second, adults frequently imitate younger humans (Papousek & Papousek, 1989; Field, Guy, & Umbel, 1985). Third, events in the environment may lead to similar reactions in oneself and others at the same time, for example, if something unpleasant is present in the environment most will produce a facial reaction of disgust. One can therefore observe a disgusted face at the same time as producing one. Fourth, vertical associations can be established indirectly through common associations with other representations of action. For example, verbal representations of action may mediate visual and motor associations; one may often hear the word 'frown' when frowning oneself and also when observing someone else frown. Through common associations with the word 'frown', associations may form between the visual and motor representations of a frown.

The ASL model proposes that novel action sequences can be imitated through additional processes which are not unique to imitation (Heyes & Ray, 2000). This 'novel' imitation is possible because an observed action can be broken down into constituent movement primitives which are familiar. The sequence of these primitives is learned through processes which operate whenever a subject learns a sequence of visual stimuli (forming 'horizontal' associations). When this visual sequence is learned, it is possible to imitate this novel sequence through pre-existing vertical associations between visual and motor representations of the familiar movement primitives.

Keysers & Perrett (2004) have proposed a neurophysiological version of the ASL model, describing how learning between visual and motor representations of action may be instantiated in the brain. They suggest that associative links may form between visual representations of action in the superior temporal sulcus (STS), and motor representations in inferior parietal and premotor cortices. There is evidence that STS is reciprocally connected with the inferior parietal lobule, which in turn has strong reciprocal connections with premotor cortex. Through these links, parietal and premotor neurons, which once only fired during execution of action, may also come to fire when observing action.

1.2.4 Evidence distinguishing theories of imitation

It may be possible to distinguish AIM and ASL models of imitation in several ways. For example, some authors have proposed that AIM and ASL models make different predictions concerning the effector specificity of action representation in mechanisms mediating imitation (Bird & Heyes, 2005) and whether actions can be learned through observation without awareness of learning (Bird, 2003). However, the issue which will be explored in this thesis concerns whether imitation mechanisms are innate (AIM) or acquired through experience (ASL). In the remainder of this section, I therefore review studies bearing on the question of whether the capacity to imitate is innate or learned. Several features of imitation could distinguish between nativist and empiricist hypotheses. The three features which will be discussed here are presence of imitation in non-human animals, presence of imitation in infants and effects of training and expertise on imitation.

1.2.4.1 Non-human animals

If species which are close genetic relatives to humans can imitate, this could provide evidence to support the nativist hypothesis. Although there is no evidence of imitation in macaque monkeys where mirror neurons were discovered, studies have found evidence of imitation in chimpanzees (Custance et al., 1995), capuchin monkeys (Custance, Whiten, & Fredman, 1999) and marmosets (Voelkl & Huber, 2000; Bugnyar & Huber, 1997).

However, evidence of imitation in other primates would provide strong support for a nativist position only if the primates lack the opportunity for imitation-relevant learning or if more distant relatives, who also have similar experiences, do not possess similar imitative abilities. There is no evidence suggesting that primates lack the opportunity for imitation-relevant learning. In addition, there is evidence of imitation in birds (Campbell, Heyes, & Goldsmith, 1999; Akins & Zentall, 1998; Lefebvre, Templeton, Brown, & Koelle, 1997; Akins & Zentall, 1996). It is therefore difficult to argue that other primates imitate because they are close genetic relatives to humans, possessing similar innate mechanisms. Common imitation-relevant experience may have provided both humans and other primates with the ability to imitate.

1.2.4.2 Early development

Nativist and empiricist hypotheses make different predictions concerning whether experiences during life are sufficient to explain imitative abilities. If there is strong evidence to suggest that newborn infants can imitate, when they have had little opportunity to form visuomotor links through experience, this would suggest that imitation and supporting mechanisms may be innate. However, if newborns cannot imitate, imitation may be learned.

Meltzoff & Moore first reported in 1977 that if an infant aged 12-21 days old observes a caregiver protruding their tongue or opening their mouth, they will be more likely to subsequently protrude their tongue or open their mouth, respectively, rather than produce the alternative action. These authors later found that even newborn infants (mean age = 32 hours) exhibited imitative facial gestures similar to older infants (Meltzoff & Moore, 1983; 1989) and several other studies have provided support for the claim that neonates imitate (Heimann, 1989; Heimann, Nelson, & Schaller, 1989; Kaitz, Meschulach-Sarfaty, Auerbach, & Eidelman, 1988; Reissland, 1988; Vinter, 1986; Kugiumutzakis, 1985; Field et al., 1983; Field, Woodson, Greenberg, & Cohen, 1982). Meltzoff & Moore (1997) claim that these studies have demonstrated that infants imitate a wide range of gestures within the first two months of life. These include tongue protrusion, lip protrusion, mouth opening, hand gestures, head movements, eye blinking, cheek and brow motions, and components of emotional expressions.

However, despite the large number of studies claiming to demonstrate evidence for neonatal imitation, the effect has not always been replicated. It fact, there may only be good evidence for neonatal imitation of tongue protrusion (Anisfeld et al., 2001; Ullstadius, 1998; Anisfeld, 1996; Anisfeld, 1991) and even this may result from simple arousal (Jones, 1996; 2006). Anisfeld (1991; 1996) discussed evidence that tongue protrusion is the only gesture which is reliably imitated in infants. He notes that previous data do not really provide evidence for imitation of other actions; studies have simply looked for two-way interactions between observed and executed action type, where tongue protrusion was one of the actions. A two-way interaction has been interpreted as evidence of imitation of both actions, but imitation of only tongue protrusion could have created these two-way interactions. Jones (1996; 2006) hypothesised that even imitation of tongue protrusion may in fact result from arousal, suggesting that infant imitation may be supported by different mechanisms to adult imitation. Tongue protrusion acts appear more interesting to infants than other actions (Jones, 1996), and infants will protrude their tongue to other arousing stimuli such as music (Jones, 2006) and flashing lights (Jones, 1996).

Providing further support for the hypothesis that neonatal imitation is driven by arousal and therefore supported by different mechanisms to adult imitation, there is a developmental gap at approximately three months in which tongue protrusion imitation, which is present in younger infants, ceases to be evident (Heimann et al., 1989). This could result from a sudden lack of motivation to imitate, but it is more likely to indicate that the structures supporting imitation in neonates differ from those supporting imitation in adults (see Johnson & Morton, 1991; Morton & Johnson, 1991). Using neonatal imitation as support for a nativist hypothesis of adult imitation mechanisms would therefore require additional demonstration that neonatal imitation displays similar characteristics to adult imitation.

A study investigating correlations in imitative ability between monozygotic and dizygotic two-year-old twins suggests a modest genetic contribution towards imitation; correlations in imitative ability were found to be greater amongst monozygotic twin pairs than amongst dizygotic twin pairs (McEwen et al., in press). However, the authors note that this impact is likely to be due to genetic influences on perception, attention and motivation, so cannot be used as evidence of a direct genetic influence on imitation mechanisms. Notably, the authors also found that environmental influences may be larger than genetic influences; correlations in imitative abilities in dizygotic twin pairs were more than half those correlations in monozygotic twin pairs.

1.2.4.3 Training and expertise

The empiricist ASL model would predict a large influence of training and expertise on imitation, because it is 'training' which has provided us with those imitative abilities which we possess. In contrast, the nativist AIM model should predict little influence. Although the operation of innate mechanisms could, in principle, by modified by experience, Pinker (1997) argues that experience-based alteration of innate mechanisms would usually be maladaptive, and therefore that natural selection is likely to have acted to prevent such modification. In a similar vein, Cosmides & Tooby (1994) suggest that innate mechanisms are 'buffered against most naturally occurring variations in the physical and social environment' (p.69), and Lorenz (1965) states that inherited aspects of behaviour can be identified as the 'least changeable' (p.35). This reasoning is consistent with evidence that mechanisms which are widely thought to be innate are found to remain constant in the face of differing experience. For example, Zago & Lacquaniti (2005) found that expectations that objects fall at a rate determined by gravity could not be modified when presenting participants with different spatiotemporal parameters.

Evidence from several behavioural studies shows that, as the ASL model predicts, familiar actions are imitated more successfully than novel actions (Tessari & Rumiati, 2004; Rumiati & Tessari, 2002). Participants made fewer errors when imitating actions such as combing the hair or brushing the teeth, compared with control novel actions, where similar movement components were executed on a different part of the body (e.g. on the arm). In a follow-up investigation, the authors found that when participants practised imitating novel actions, they were subsequently imitated with the same accuracy as previously familiar actions (Tessari, Bosanac, & Rumiati, 2006).

These experiments indicate an influence of experience on imitation, but they do not discriminate between sources of variation in motor experience, perceptual experience and correlated visuomotor experience. Familiar actions will have been observed more often than novel actions, they will have been performed more often, and they will have been performed more often whilst concurrently observing the same actions. The ASL model predicts that it is correlated visuomotor experience which is important for the development of imitation. To use effects of experience as support for the ASL model therefore requires distinguishing effects of motor and perceptual experience, from those of correlated visuomotor experience.

A training study conducted by Heyes et al. (2005) controlled for levels of perceptual and motor experience, and observed effects of correlated visual and motor experience. During a training phase, Heyes et al. (2005) required half of their participants to open their hand whenever they detected a stimulus hand begin to open, and to close their hand whenever they detected a stimulus hand begin to close. These participants therefore performed responses which were compatible with the stimuli. The other half of participants were required to make responses which were incompatible with stimuli, that is, to open their hand whenever the stimulus hand closed and to close their hand whenever the stimulus hand opened. Therefore, the two groups performed both responses equally often, and observed both stimuli equally often. However, the relationship between the stimuli and responses differed between the two groups. In a subsequent test session, participants in the compatible training group showed an automatic imitation effect; in a simple RT task, participants were faster to execute a pre-specified action (e.g. opening the hand) when it was compatible with the observed action (opening) rather than incompatible (closing). In contrast, those participants who received incompatible training did not show an automatic imitation effect. This result suggests that training can influence imitation of a stimulus, and that these influences of training are likely to result from associative learning about the relationship between visual stimuli and motor responses.

Functional imaging studies support the hypothesis that training and experience can influence the operation of imitation mechanisms; activation in parietal and premotor cortex which arises when observing an action is influenced by expertise in performing the observed action. Calvo-Merino, Glaser, Grezes, Passingham, & Haggard (2005) conducted an fMRI study with expert ballet and capoeira dancers to investigate influences of experience on activation of motor cortices when observing action. The authors found that when participants (e.g. ballet dancers) were observing dance actions which they had been trained to perform (ballet movements), there was greater activation in premotor and parietal cortices than when observing actions which they had not been trained to perform (capoeira movements). Cross, Hamilton, & Grafton (2006) observed similar effects of expertise in dancers, finding that observing actions which dancers rated that they could perform well elicited greater left premotor and parietal activation, compared with observing actions which they rated that they performed badly. Haslinger et al. (2005) found similar effects of expertise in pianists. When pianists observed a subject play the piano, there was greater activation in premotor and parietal cortices, relative to when controls observed a subject play the piano, and relative to when pianists observed serial finger-thumb opposition movements.

In line with the behavioural findings of Rumiati & Tessari (Tessari et al., 2006; Tessari & Rumiati, 2004; Rumiati & Tessari, 2002), Grezes et al. (1998) also found that highly familiar actions activate premotor cortex to a greater extent than less familiar actions. Furthermore, effects of experience have been found in premotor and parietal cortices when observing tool use. Ferrari, Rozzi, & Fogassi (2005) found that neurons in the monkey premotor cortex discharge when the monkey observes an experimenter use a stick or a pair or pliers, but only following training where it observes such tool use whilst performing actions itself. Järveläinen, Schurmann, & Hari (2004) even found that amount of experience with chopsticks in humans, according to self-report, correlated with the degree of primary motor cortex activation when observing their use.

In summary, the studies reviewed in this section indicate that training and expertise can have a significant impact on imitative capabilities and imitation mechanisms. However, only one study has explicitly dissociated correlated visuomotor experience from motor experience and perceptual experience (Heyes et al., 2005). Therefore, alongside the inconclusive findings from research with non-human animals (section 1.2.4.1) and human neonates (section 1.2.4.2), it is apparent that there is currently very little evidence which favours the AIM model over the ASL model, or vice versa.

1.3 Human imitative bias

Evidence is accumulating that naturally occurring movements of the human body are especially effective in eliciting motor activation and explicit imitative responses. This 'human imitative bias' may provide a tool for investigating theories of imitation. Section 1.3.1 reviews evidence of a human imitative bias, and section 1.3.2 discusses potential explanations for the bias.

1.3.1 Evidence

There is some developmental evidence that human action stimuli are more effective in eliciting imitative responses than robotic stimuli, even when robotic stimuli are closely matched in many respects to their human counterparts. Legerstee (1991) presented five to eight week old infants with human or mechanical mouth opening movements and tongue protrusions. The infants subsequently reproduced mouth and tongue movements following human demonstration, but not following mechanical demonstration. Abravanel & DeJong (1991) similarly presented five and 12 week old infants with similar movements made by human and mechanical models and found successful reproduction of tongue movements performed by a human model, but not by a mechanical model.

Differences in imitation of human and robotic movement have also been observed in adults. In an interference paradigm, Castiello, Lusher, Mari, Edwards, & Humphreys (2002) found that observing human, but not robotic, movements influenced subsequent performance of similar reaching and grasping movements. Movement dynamics differ as a function of the size of an object to be grasped. When participants grasped objects, the movement dynamics were influenced by the size of an object which an observed human model had previously grasped, but not the size of an object which an observed robotic model had previously grasped. Castiello (2003) similarly found that a distractor object which was present when a human model grasped a target object and influenced the human model's movement dynamics also influenced the movement dynamics of an observing participant who subsequently grasped the same target object in the absence of the distractor object. In contrast, the presence of a distractor object when a robotic model grasped a target object did not influence movement dynamics of the observing participant.

Using an automatic imitation paradigm of a different kind, Kilner, Paulignan, & Blakemore (2003) and Oztop, Frankline, & Chaminade (2004) found a stronger tendency to imitate human than robotic movements. Participants in both studies were required to perform sinusoidal arm movements in one direction (e.g. vertical) whilst simultaneously observing human or robotic arm movements in a congruent (vertical) or incongruent direction (horizontal). Participants displayed more variance in the pathway of movements when concurrently observing human movements in an incongruent direction, compared with a congruent direction. However, this automatic imitation effect was found to be smaller (Oztop et al., 2004), or not present (Kilner et al., 2003), when concurrently observing robotic movements. This was despite manufacturing the robotic model to appear human, with a head, trunk, arms and legs.

An fMRI study has supported the idea that human movement stimuli are more readily imitated than robotic movement stimuli, by finding that, relative to robotic movement, observing human movement generates more activation of cortical areas thought to mediate imitation. Tai, Scherfler, Brooks, Sawamoto, & Castiello (2004) instructed participants to observe a human or robot model, as it either grasped an object or remained static. The authors found greater left premotor activation when observing human movement than when observing a static control, but did not find greater activation when observing robotic movement relative to a static control.

Other imaging studies have suggested that observing natural human movement may activate motor representations of movement more than observing unnatural human movement or animal movement. Stevens, Fonlupt, Shiffrar, & Decety (2000) compared motor cortical activation when participants observed natural human movements and impossible human movements. Participants were presented with two images; one of an arm on one side of a leg and one of the arm on the other side. If the images were presented at one speed, the arm appeared to move through the leg (impossible), and if the images were presented at another speed, the arm appeared to move round the leg (possible). They found that activation in primary motor cortex and the superior parietal gyrus was greater when participants observed possible movement than when they observed impossible movement. In addition, Buccino et al. (2004) found greater activation in premotor and parietal cortices when participants observed human biting actions, compared with biting actions made by dogs or monkeys.

In summary, these studies indicate that human movement stimuli evoke imitative responses and activate cortical areas thought to mediate imitation to a greater extent than non-human movement stimuli.

1.3.2 Explaining the human imitative bias

The human imitative bias may result from either top-down or bottom-up influences on the operation of imitation mechanisms. There may be top-down modulation of the operation of these mechanisms, on the basis of knowledge about whether an observed stimulus is or is not human. This hypothesis is consistent with both AIM and ASL models of imitation. Alternatively or additionally, the human bias may be driven by perceptual properties of the stimuli. The bottom-up modulation account is also consistent with both AIM and ASL models, but the two models make different predictions concerning whether the bias can be modulated.

The AIM model of imitation would suggest that any stimulus-driven difference in imitation of human and non-human stimuli is innate. Many researchers, including Meltzoff, the author of the AIM model, have proposed that imitation mechanisms evolved to facilitate higher sociocognitive functions such as theory of mind (e.g. Kilner et al., 2003; Meltzoff & Decety, 2003; Gallese & Goldman, 1998). Because humans have mental states and non-humans are less likely to, imitation mechanisms may have evolved such that they will preferentially process human input. It is possible that a mechanism evolved such that this modulation would be performed top-down; a mechanism could have evolved whereby higher-level mechanisms involved in social inferences modulate operation of imitation mechanisms on the basis of knowledge about whether a stimulus is human or not. It is also possible that instead, this modulation is a result of the specific perceptual properties of the stimuli. The AIM model may therefore predict that the imitation module is tuned through evolution to only allow access to stimuli with human perceptual properties.

However, greater imitation of stimuli with human properties is also consistent with the ASL model of imitation. Opportunities for forming associations between human stimuli and matching responses are presumably far greater than those for forming associations between non-human stimuli and matching responses; we will perform actions whilst also observing compatible human actions quite frequently (see section 1.2.3), whereas we will not often perform actions whilst observing compatible non-human movements. If imitative abilities develop through associative learning, then the preference for human stimuli may result from greater opportunity for associative learning with these stimuli.

The experiments in Chapter 3 investigate whether the human imitative bias results from top-down or bottom-up influences on operation of imitation mechanisms. The experiments use a stimulus-response compatibility paradigm, on the assumption that this paradigm reflects automatic imitation (an assumption tested in Chapter 2). They present participants with stimuli which are either human or robotic, and differentially inform participants that stimuli are human or robotic. If the top-down hypothesis is correct, then automatic imitation effects should be larger with stimuli believed to be human than stimuli believed to be robotic, regardless of actual identity. However, if the imitative preference for human stimuli is created through perceptual properties of the stimuli, automatic imitation effects should be larger with genuinely human stimuli than genuinely robotic stimuli, regardless of beliefs about identity.

On the basis of evidence in Chapter 3 that the human imitative bias is driven by perceptual properties of the stimuli, Chapter 4 attempts to distinguish the AIM and ASL predictions concerning this bias. The experiments in this chapter therefore assess the effects of executing actions which are either compatible or incompatible with movement of robotic stimuli, on automatic imitation of robotic stimuli and the human imitative bias. If imitative abilities and the human imitative bias are innate (AIM), then this training should not modulate automatic imitation of robotic stimuli, and hence, the human imitative bias. However, if imitative abilities are formed through associative learning (ASL), then automatic imitation of robotic stimuli should be modulated following training which provides opportunities for associative learning, and hence the human bias should also be modulated.

1.4 Summary

Human body movements are especially effective in eliciting motor activation and explicit imitative responses. Theories have been outlined concerning why this is the case. The human imitative bias may emerge because of top-down modulation of imitation mechanisms on the basis of knowledge about whether observed stimuli are or are not human. Alternatively, the imitative bias may be driven by perceptual properties of the stimuli. Both of these views are consistent with AIM and ASL theories of imitation. However, if the bias is driven by perceptual properties of the stimuli, then the ASL model would predict that imitation of stimuli and hence, the bias, is modifiable, but the AIM model would predict that it is not. This thesis aims to distinguish these hypotheses concerning the human imitative bias on the basis of 1) whether beliefs about stimulus identity or perceptual properties drive automatic imitation of stimuli and 2) whether opportunities for associative learning with non-human (robotic) stimuli influence imitation of them and the human imitative bias. The thesis also investigates whether opportunities for associative learning can modulate visuotactile integration with human and non-human stimuli.

Chapter 2: Configural action compatibility or orthogonal spatial compatibility?

Action compatibility effects are a type of stimulus-response compatibility effect whereby responses to human action stimuli are faster when they involve execution of a matching action than when they involve execution of a non-matching action (e.g. Heyes et al., 2005; Vogt et al., 2003; Craighero et al., 2002; Brass et al., 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Kerzel & Bekkering, 2000; Stürmer et al., 2000). Types of action and notions of whether they do or do not match are defined using intuitive ordinary language categories (e.g. opening the hand, lifting a finger). For example, opening and closing hand actions are executed faster when they are compatible with an observed stimulus action than when they are incompatible, and this compatibility effect is present even when the identity of the stimulus action (opening or closing) is task-irrelevant and the response has been prepared in advance (Heyes et al., 2005).

For action compatibility effects to be relevant to the study of imitation, the effects should be driven by automatic activation of matching motor representations when observing actions. That is, compatible actions should be executed faster than incompatible actions because the correct action representation is activated through observation and therefore incorrect action representations do not need to be suppressed before the correct response can be executed. It is likely that these compatibility effects are generated through such processes, given the body of neurological evidence which suggests that observing an action automatically elicits activation in motor cortical areas involved in performance of an imitative response (see Chapter 1). If action compatibility effects are driven by these processes, the paradigm seems an ideal candidate for investigating imitation in this thesis, because mechanisms which solve the correspondence problem can be investigated in the absence of other social processes which may mediate intentional imitation (see Chapter 1).

However, the possibility has recently been raised that action compatibility effects may reflect spatial compatibility rather than action compatibility (e.g. Berthenthal, Longo, & Kosobud, 2006; Brass et al., 2001). Spatial compatibility is a form of stimulus-response compatibility which refers to the finding that actions are executed faster in response to stimuli which are in a similar relative spatial location to the response hand (see Umilta & Nicoletti, 1990; Fitts & Deininger, 1954) or which appear to move towards the response hand (Bosbach, Prinz, & Kerzel, 2004; Proctor, van Zandt, Lu, & Weeks, 1993; Michaels, 1988). When participants are instructed to press a key on the left of their body, egocentrically defined, in response to a red light and a key on the right in response to a green light, they are faster to execute these responses when the stimuli are presented on the same, rather than the opposite, side of their body as the required response (Umilta & Nicoletti, 1990). Bosbach et al. (2004) also found that the movement direction of stimuli can produce spatial compatibility effects. The authors required participants to press keys on the left and right of their body in response to whether a moving sine-wave grating displayed broad or narrow stripes. Responses were faster when the response-irrelevant direction of motion was towards the correct response key rather than towards the incorrect key.

On some level, action compatibility effects must be mediated by spatial compatibility, because actions will match if the spatial features of the actions match. However, spatial information can be encoded in many different coordinates (e.g. Palmer, 1989; Corballis, 1988; Hinton & Parsons, 1981), and compatibility between stimuli and responses on only certain spatial coordinates is likely to mediate action compatibility. Three types of spatial coordinate will be outlined here, along with discussion of whether compatibility on these coordinates is likely to mediate action compatibility.

First, allocentric spatial codes specify where a stimulus or response is located with reference to an object. For example, Hommel & Lippa (1995) found that responses on one side of space (e.g. left of the body, egocentrically defined) are faster to stimuli which are spatially compatible with the required response according to location on a reference stimulus (left of the stimulus) rather than to stimuli which are spatially incompatible (right of the stimulus). These allocentric spatial codes are unlikely to mediate action compatibility effects of the type usually investigated; the actions tend to be intransitive, so there are few candidate stimuli which could serve as reference frames for the movements. For example, two studies have observed action compatibility effects with opening and closing hand movements (e.g. Heyes et al., 2005; Stürmer et al., 2000), where the movement is not directed towards an object and there are no other clearly visible objects in the room.

Second, egocentric spatial codes specify where a stimulus or response is located with reference to a certain body part. The stimulus or response can be encoded as left, right, up or down relative to many body parts, for example, the head or the torso (e.g. Buneo & Andersen, in press; Pellijeff, Bonilha, Morgan, McKenzie, & Jackson, in press; Gross & Graziano, 1995). These egocentric spatial codes may mediate action compatibility; an action may be more compatible with an observed action if both actions move in the same direction relative to the torso, head or other effectors. However, it seems unlikely that imitation and action compatibility are entirely mediated by these simple egocentric spatial codes. We are able to imitate when we are oriented differently to an observed party. If someone points their left foot out to their left side when facing us, we are able to subsequently point our left foot out to our left side despite our leg moving in a direction which is opposite to that which is observed. In fact, Wapner & Cirillo (1968) found that by adulthood, when the experimenter is facing participants, participants are more likely to subsequently move effectors which are anatomically corresponding rather than simple spatially egocentrically corresponding. 80-85% of the time, when the experimenter touched his left or right ear with his left or right hand, and said 'do as I do', participants would touch the anatomically matching ear with the anatomically matching hand, despite these responses being spatially incompatible with those observed on simple egocentric dimensions.

A third type of spatial code may explain our ability to imitate in such situations. There is evidence that the spatial properties of stimuli and responses can also be processed configurally. These codes can specify whether effectors are moving apart from each other or towards each other, therefore effectively specifying how bodies change shape. Simple spatial information concerning whether something moves to the left or right of our body may be lost in these codes because evidence suggests that configural representations can be rotation-invariant (cf. face processing, Yovel & Kanwisher, 2005; Rhodes et al., 2004; Bentin, Allison, Puce, Perez, & McCarthy, 1996; Perrett et al., 1985). Specifically, there is evidence that STS representations of observed actions may be configural. For example, Thompson, Clarke, Stewart, & Puce (2005) found that STS activation was equivalent when observing an upright or inverted walker (cf. Grossman & Blake, 2001). Perrett and colleagues have also found that the firing rate of many neurons in STS does not distinguish viewpoint (e.g. Jellema & Perrett, 2006; Oram & Perrett, 1996; Perrett et al., 1991; Perrett et al., 1989; Perrett et al., 1985), or left from right arm movement (Jellema, Baker, Wicker, & Perrett, 2000). In addition, single-cell research with monkeys and imaging studies with humans have suggested that premotor cortical representations of action (part of the proposed candidate neurological mechanism of imitation in Chapter 1) are spatially configural; activation levels differentiate types of grip performed (e.g. precision) and not whether the action was on the right or left relative to other effectors (e.g. Johansen-Berg et al., 2002; Schluter, Krams, Rushworth, & Passingham, 2001; Schluter, Rushworth, Passingham, & Mills, 1998; Gallese et al., 1996; Rizzolatti et al., 1996).

The first widely cited study which investigated action compatibility confounded simple egocentric spatial compatibility with configural spatial compatibility, and therefore did not determine whether configural spatial compatibility contributed toward the effects. In a choice RT procedure, Stürmer et al. (2000) required participants to open or close their hands whenever they detected a video stimulus hand change colour (e.g. open their hand when it turned red and close their hand when it turned blue). Participants were faster to perform a required response (e.g. opening their hand) when the task irrelevant stimulus, a configural action type, was compatible with the required response (opening) than when it was incompatible (closing). However, both stimulus and response actions were arranged along a horizontal axis. This arrangement meant that stimuli were compatible with responses on both configural and simple egocentric spatial dimensions; when both stimulus and response hands opened the fingers moved upwards, and when they closed the fingers moved downwards (see Figure 1A). Compatibility effects may have been generated either through compatibility of configural action types (e.g. opening movement) or through compatibility of egocentric movement directions (e.g. upwards movement).

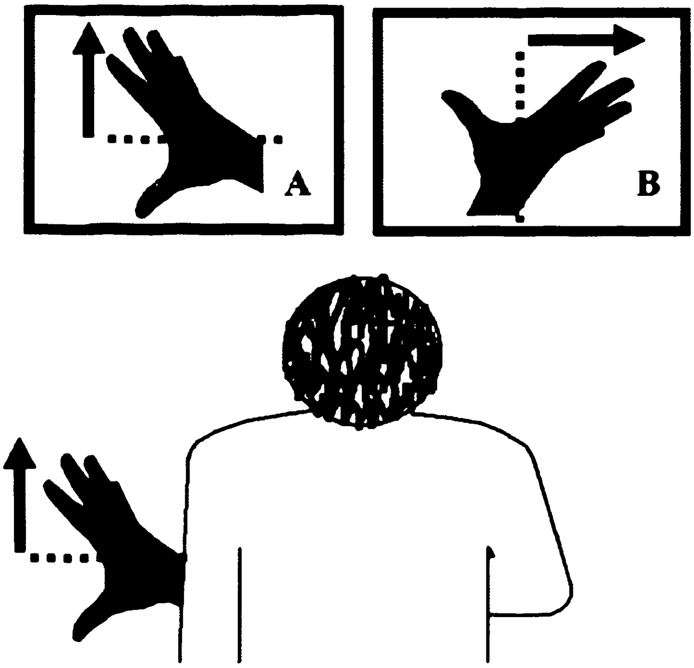


Figure 1: The stimulus and response movement direction in Stürmer et al. (2000) (A) and Heyes et al. (2005) (B). When participants opened their hand, their fingers moved upwards and when they closed their hand, their fingers moved downwards. In the experiments of Stürmer et al. (2000), this was also the case when the stimulus hand opened and closed. In contrast, in the experiments of Heyes et al. (2005), when the stimulus hand opened, the fingers moved to the right, and when the stimulus hand closed, the fingers moved to the left.

More recent investigations of action compatibility have attempted to dissociate simple egocentric and configural compatibility between observed and executed actions. In a simple RT procedure, Brass et al. (2001) found that participants were faster to execute a pre-specified index finger action (e.g. lifting movement, moving upwards) in response to an action compatible movement of a stimulus index finger (lifting movement, moving upwards), rather than an action incompatible movement (tapping movement, moving downwards). They performed an additional experiment to investigate whether simple egocentric or configural spatial codes were mediating compatibility effects. They flipped the stimulus hand in a horizontal plane such that configural lifting finger actions moved downwards in the stimulus display, and tapping finger actions moved upwards. In this experiment, responses which were compatible with the stimulus on configural spatial codes were incompatible on simple egocentric spatial codes. In spite of this, the results showed a compatibility effect generated by configural spatial codes; finger actions (e.g. lifting) were executed faster when the observed configural action type was compatible with the required action (lifting) than when it was incompatible (tapping). However, compatibility effects were larger when movements were arranged such that responses which were compatible with the stimulus on configural spatial codes were also compatible on simple egocentric spatial codes, suggesting that both simple egocentric and configural spatial codes may contribute towards action compatibility.

Heyes et al. (2005) attempted to dissociate configural and simple egocentric spatial compatibility by removing simple egocentric compatibility rather than arranging the two types of compatibility in opposition. Removing simple egocentric compatibility is preferable to arranging the two types of compatibility in opposition for two reasons. First, if there are differences in compatibility effects between two conditions, one can conclude that the differences are driven by levels of configural compatibility rather than levels of simple egocentric compatibility. Second, because something configurally compatible is not necessarily simple egocentrically incompatible, the paradigm can be more sensitive to configural compatibility.

Heyes et al. (2005) required responses to be made along a spatial axis which was orthogonal to that of the stimulus hand, that is, responses were made along a horizontal axis and stimulus movements were arranged along a vertical axis (see Figure 1B). In a simple RT paradigm, participants were required to open or close their hand whenever they detected a stimulus hand start to open or close. Participants were faster to execute an action (e.g. to open their hand, fingers move upwards) in response to configurally compatible (opening, fingers move to the right) rather than incompatible stimulus movements (closing, fingers move to the left). Heyes et al. (2005) viewed it as unlikely that compatibility on simple egocentric spatial codes was creating observed compatibility effects because stimulus and response movements were arranged along orthogonal simple egocentric dimensions. They therefore assert that configural compatibility was driving the compatibility effects.

However, several studies have reported orthogonal simple egocentric spatial compatibility. Typically, 'up-right/down-left' advantages have been found; participants are faster to execute responses to stimuli when the stimulus-response relationships consist of up-right/down-left mappings rather than down-right/up-left mappings (e.g. Lippa & Adam, 2001; Proctor & Pick, 1999; Lippa, 1996; Hommel & Lippa, 1995; Bauer & Miller, 1982). For example, Lippa (1996) found that participants were faster to execute key presses in response to 'X' stimuli presented on a computer screen if key presses to the right were required in response to stimuli presented above fixation (up) and key presses to the left were required in response to stimuli presented below fixation (down), than if right key presses were required in response to down stimuli and left key presses were required in response to up stimuli.

There is no consensus concerning the processes which mediate orthogonal spatial compatibility effects (e.g. Cho & Proctor, 2005; Cho & Proctor, 2004; Cho & Proctor, 2003; Lippa & Adam, 2001; Adam, Boon, Paas, & Umilta, 1998; Hommel & Lippa, 1995). Some propose that the effects result from salience of spatial dimensions; up and right are more salient than down and left (Just & Carpenter, 1975), and effects are driven by compatibility in salience (e.g. Cho & Proctor, 2005). Others have proposed that the effects result from properties of the motor system. Lippa & Adam (2001) suggest that the response dimension is mentally rotated such that it matches the stimulus dimension, and the direction of rotation is determined by the direction which would result in the most comfortable end-state if the effector were actually rotated.

Orthogonal spatial compatibility is unlikely to mediate action compatibility for two reasons. First, there is no evidence, either behavioural or neurological, that observing an action moving to the right is more likely to activate motor representations of upward, rather than downward actions, and that observing an action moving to the left is more likely to activate motor representations of downward, rather than upward, actions. Second, there is not an intuitive sense of match between upward and rightward actions and downward and leftward actions. This is reflected by definitions of match in the action compatibility and imitation literature; match is usually defined in configural spatial terms (e.g. opening the hand, opening the mouth), and a match in 'salience', if this is what drives orthogonal spatial compatibility effects, would not tend to be classed as an imitative match. However, without greater understanding of what drives orthogonal spatial compatibility and explicit exploration of whether observing actions activates motor representations of orthogonally spatially compatible actions, it is not possible to rule out the possibility that orthogonal spatial compatibility can mediate action compatibility.

The experiments reported in this chapter used the methods employed by Heyes et al. (2005) to investigate whether the compatibility effects which they observed with opening and closing hand actions are a result of orthogonal spatial compatibility or configural action compatibility. These experiments had two purposes. First, they would allow further investigation of whether action compatibility can, in principle, be mediated by configural codes of action, allowing greater understanding of representations of action in mechanisms mediating imitation. Second, addressing whether these specific effects reflect configural compatibility or orthogonal spatial compatibility could establish whether the paradigm is appropriate for investigating the mechanisms which mediate imitation in subsequent experiments in this thesis. Although it is not possible to rule out the possibility that orthogonal spatial compatibility mediates action compatibility, it is more likely that configural spatial compatibility mediates action compatibility. That is, observing an action has previously been found to activate motor representations of configurally matching actions (e.g. Brass et al., 2001; Gallese et al., 1996; Rizzolatti et al., 1996; Wapner & Cirillo, 1968), and there is an intuitive sense of match between the actions, reflected by the definitions of match used in the action compatibility and imitation literature and participants producing configurally compatible actions when told to 'do as I do' (Wapner & Cirillo, 1968).

Like Heyes et al. (2005), Experiments 1 and 2 required participants to open or close their hand in a horizontal axis, in response to opening and closing stimulus hand movements arranged along a vertical axis. To dissociate contributions of simple egocentric and configural compatibility, compatibility effects were compared when stimulus configural action types (opening or closing) moved in different simple egocentric directions. That is, stimulus movements were either arranged similarly to those in the studies of Heyes et al. (2005), such that fingers moved to the right when opening and to the left when closing, or they were flipped in a vertical axis such that fingers moved to the left when opening and to the right when closing. If compatibility effects are driven by orthogonal spatial compatibility, then compatibility effects would be expected to be similar when simple egocentric spatial properties are the same as those in Heyes et al. (2005) but to reverse when simple egocentric spatial properties reverse. In contrast, if the effects result from configural action compatibility, then compatibility effects would be expected to be similar to those in Heyes et al. (2005) regardless of simple egocentric spatial properties.

2.1 Experiment 1

In Experiment 1 participants were required to respond to an anatomically right stimulus hand either viewed from the front (thumb on left when upright), as in the experiments reported by Heyes et al. (2005), or viewed from the rear (thumb on right if upright). When a stimulus hand viewed from the front opened, the fingers moved to the right of the participant's midline, and when it closed, the fingers moved to the left. The converse was true when a hand was viewed from the rear; when it opened, the fingers moved to the left, and when it closed, the fingers moved to the right.

If compatibility effects observed by Heyes et al. (2005) were due to orthogonal spatial compatibility, then in the present experiment one would expect that effect to be replicated in the front view condition, and to be reversed in the rear view condition. One would expect actions (e.g. opening the hand) to be executed faster in response to configurally compatible (opening), rather than incompatible (closing), stimulus actions in the front view condition, and to be executed faster in response to configurally incompatible, rather than compatible, stimulus actions in the rear view condition. In contrast, if the effect observed by Heyes et al. (2005) was driven by configural action compatibility, then one would expect that effect to be replicated in both front and rear conditions in Experiment 1. Actions (e.g. opening the hand) should be executed faster in response to configurally compatible (opening), rather than incompatible (closing), stimulus actions in both front and rear view conditions.

2.1.1 Method

Participants

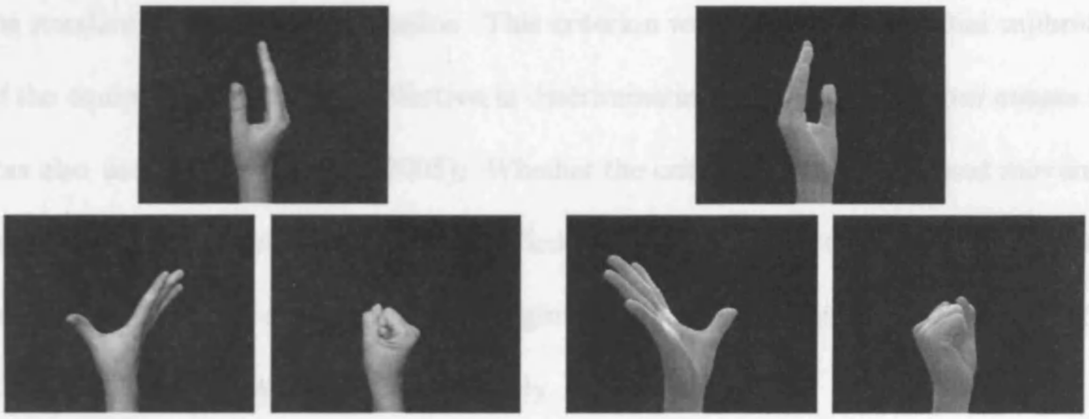
Seventeen consenting, healthy volunteers with an average age of 25.2 years, six male, participated in Experiment 1, and were paid a small honorarium for their participation. The data from one participant was removed from the analysis because less than 90% of their data was remaining following the employment of various exclusion criteria (see below).

All participants were right-handed, had normal or corrected-to-normal vision, and were naïve with respect to the purpose of the experiment. These criteria were also met in all subsequent experiments in this thesis.

Stimuli

All stimuli were presented on a computer screen (60Hz, 400mm, 96DPI), in colour on a black background, and viewing was unrestrained at a distance of approximately 600mm.

The stimuli can be seen in Figure 2. Each imperative stimulus was an anatomically right hand either opening or closing, viewed from either the angle at which one normally views ones own hands (front, thumb on the left) or the opposite angle (rear, thumb on the right). Both movements began with the fingers closed and pointing upwards in parallel with the thumb (warning stimulus). The warning stimulus occupied approximately 6.5° of visual angle horizontally and 17.0° vertically. In the opening movement, the fingers and thumb splayed, and, in the closing movement, they rolled into a fist. The last frame of the opening stimulus movement occupied approximately 14.3° of visual angle horizontally and 17.1° vertically, whereas the last frame of the closing stimulus movement occupied approximately 6.6° horizontally and 12.6° vertically. Each movement consisted of 12 frames and lasted for 480ms. The hands appeared approximately life-sized.



Open Close Open Close

A Front view B Rear view

Figure 2: The stimuli used in Experiment 1. A Front View, B Rear View. Within each stimulus type, the top image is the warning stimulus and the two images below are the last frame of the hand opening video (left) and the last frame of the hand closing video (right).

Data recording and analysis

For both open and close responses, response onset was measured by recording the electromyogram (EMG) from the first dorsal interosseus muscle using disposable Ag/AgCl surface electrodes. Signals were amplified, high-pass filtered at 20Hz, mains-hum filtered at 50Hz and digitised at 2.5kHz. They were rectified and smoothed using a dual-pass Butterworth filter, with a cut-off frequency of 50Hz. Signals were not low-pass filtered. To define a baseline, EMG activity was registered for 100ms when the participant was not moving at the beginning of each trial. A window of 20ms was then shifted progressively over the raw data in 1ms steps. Response onset was defined by the beginning of the first 20ms window after the imperative stimulus in which the standard deviation for that window, and for the following 20ms epoch, was greater than 2.75 times the standard deviation of the baseline. This criterion was chosen during initial calibration of the equipment as the most effective in discriminating false positives from misses and was also used by Heyes et al. (2005). Whether the criterion correctly defined movement onset in the present experiment was verified by sight for every trial performed by each participant. Stimulus onset marked the beginning, and EMG onset marked the end, of the RT interval. Errors were recorded manually.

Procedure

Participants were tested individually in a dimly lit room. The participant's right forearm lay in a horizontal position across his/her body, parallel with the stimulus monitor. It was supported from elbow to wrist by an armrest, and the participant's hand was free to move. The wrist was rotated so that the fingers moved upwards during opening responses, and downwards during closing responses. Therefore, given that stimulus movements were presented in the lateral plane (left-right), response movement direction was orthogonal to stimulus movement direction (see Figure 1). After making each response, participants were required to return their hand to a neutral starting position.

In each block of the simple RT task, participants were required to make a pre-specified response (to open or to close their right hand) as soon as the stimulus hand began to move. There were two blocks in which closing was the required response and two in which opening was the required response, and participants were instructed about the required response in each block at its outset. The two blocks requiring the same response type were completed in immediate succession. Participants were instructed to refrain from moving their hand in catch trials, when the stimulus hand did not move.

All trials began with presentation of the warning stimulus. In stimulus trials, this was replaced 800, 1600 or 2400ms later by onset of the opening or closing stimulus, which was of 480ms duration. After the imperative stimulus movement, the screen went black for 3000ms before the warning stimulus for the next trial appeared. In catch trials, the warning stimulus remained on the screen for 2880ms before the 3000ms inter-trial interval. Each block presented, in random order, 60 stimulus trials and 12 catch trials. There were five stimulus trials of each type, defined by combination of the stimulus (opening and closing), stimulus hand view (front or rear) and stimulus onset asynchrony (SOA, 800, 1600, 2400ms) variables.

Before testing commenced in each block, participants completed 12 practice trials (five open stimulus, five close stimulus and two catch trials) with the response to be used in that block. The order in which responses were tested was counterbalanced (open first or close first).

2.1.2 Results and discussion

Participants initiated movement in 0.52% of catch trials. These data were not analysed further. Practice trials, incorrect response types (0.39%) and all RTs smaller than 100ms and greater than 1000ms (0.13%) were excluded from the analysis. There were no response omissions. On each trial, the configural action type of the stimulus was either the same as (compatible) or different from (incompatible) the pre-specified response. The RT data, shown in Figure 3, were subjected to analysis of variance (ANOVA) in which action compatibility (compatible and incompatible) and stimulus hand view (front or rear) were within-subject variables.

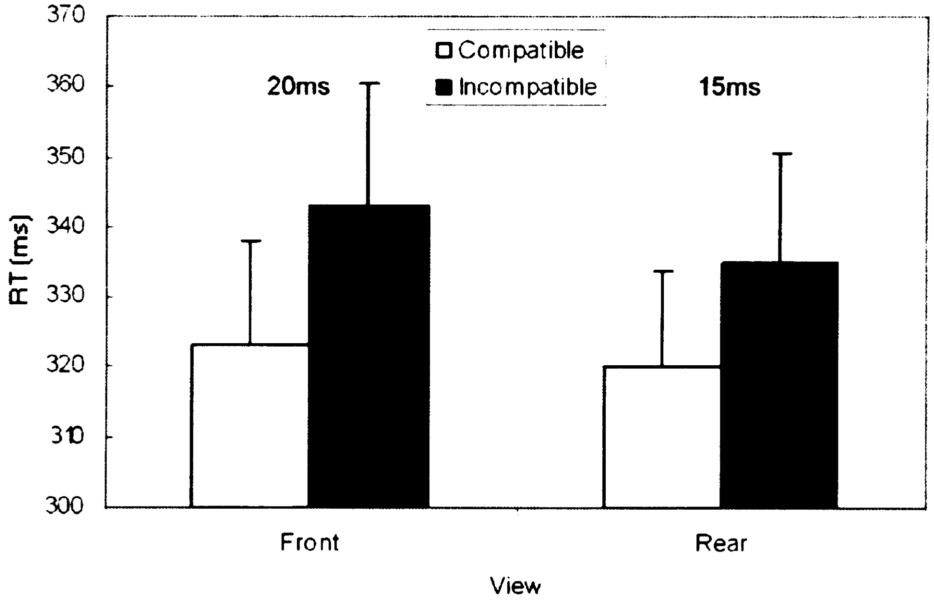


Figure 3: Experiment 1. Mean RT on action compatible (open bars) and incompatible (shaded bars) trials when the stimulus hand was viewed from the front or rear. Vertical bars indicate the standard error of the mean and numbers indicate the magnitude of the compatibility effect.

This analysis revealed a significant main effect of action compatibility (F(1,15) = 25.5, p < 0.001). On average, responding was 17ms faster when the stimulus and response action types were compatible (M = 321.8ms, SEM = 14.1ms) than when they were incompatible (M = 339.0ms, SEM = 16.5ms). This action compatibility effect was significant both when the stimulus hand was viewed from the front (F(1,15) = 19.1, p < 0.001) and when it was viewed from the rear (F(1,15) = 19.0, p < 0.001). Although the compatibility effect was numerically greater when participants viewed the stimulus from the front than from the rear, this difference was not reliable (F(1,15) = 1.3, p = 0.3).

The results of Experiment 1 provide evidence that compatibility effects with opening and closing hand movements are not due solely to orthogonal spatial compatibility. In this experiment, compatibility effects were influenced by configural action type rather than movement direction, that is, responses (e.g. opening the hand) were faster when they were compatible with the configural stimulus action type (opening) than when they were incompatible (closing), regardless of stimulus movement direction (leftward or rightward) when opening and closing. If effects were entirely generated by orthogonal spatial compatibility, then one would have expected that effects would reverse when stimulus movement direction reverses.

2.2 Experiment 2

The results of Experiment 1 suggest that it is unlikely that orthogonal spatial compatibility has solely driven compatibility effects with opening and closing hand movements, and therefore that effects are at least somewhat determined by configural action compatibility. However, a contribution of orthogonal spatial compatibility towards observed compatibility effects cannot be ruled out. Orthogonal spatial compatibility and action compatibility were not entirely independent in Experiment 1; front and rear view stimuli did not have identical configural spatial features. Given that front and rear view stimuli did not have identical configural features, the rear view stimuli may have evoked greater action compatibility than the front view stimuli and therefore orthogonal spatial compatibility generated with the front view stimuli may not have been detected. It is plausible that the rear view stimuli evoked greater action compatibility than the front view stimuli because more fingers could be seen moving in the opening rear, rather than front view, stimulus (see Figure 2).

Experiment 2 therefore compared compatibility effects between stimuli where orthogonal spatial compatibility and configural action compatibility were entirely independent. It used a different anatomically right hand stimulus to that used in Experiment 1 and created stimuli with opposite simple egocentric spatial features by flipping them in a vertical axis. In addition, Experiment 2 provided a further test of whether orthogonal spatial compatibility mediates compatibility effects by comparing effects when participants made responses in left and right hemispace. Three studies have suggested that orthogonal spatial compatibility effects are different in right and left hemispace. Weeks, Proctor, & Beyak (1995) required participants to move a toggle switch to the left or right in response to stimuli appearing above (up) or below (down) fixation. When the toggle switch was located in right hemispace, participants were faster with up-right/down-left stimulus-response mappings, whereas when responses were made in left hemispace the up-right/down-left advantage observed in right hemispace reversed to a non-significant up-left/down-right advantage. Cho & Proctor (2004) replicated these findings of an up-right/down-left advantage in right hemispace, but extended them by also finding this advantage at the body midline, and finding a significant up-left/down-right advantage in left hemispace. Cho & Proctor (2005) found similar interactions as a function of response hemispace.

This design allowed Experiment 2 to address whether there is *any* contribution of orthogonal spatial compatibility to compatibility effects observed with opening and closing hand movements. If up-right/down-left compatibility is contributing towards compatibility effects in both hemispaces, one would always expect larger compatibility effects when responding to the right, rather than left, hand stimulus. However, if orthogonal spatial compatibility differs as a function of response hemispace, one may expect larger compatibility effects when responding to the left, rather than right, hand stimulus in right hemispace and when responding to the right, rather than left, hand stimulus in left hemispace. In contrast, if compatibility effects reflect only configural action compatibility, compatibility effects should be equal when responding to left and right stimuli, both in right and left hemispaces.

2.2.1 Method

Participants

Seventeen new, consenting, healthy volunteers with an average age of 24.6 years, four male, participated in Experiment 2, and were paid a small honorarium for their participation. The data from one participant was removed from the analysis because less than 90% of their data was remaining following the employment of the various exclusion criteria.

Stimuli

Stimuli were presented using the same apparatus as in Experiment 1. Each imperative stimulus was a right or a left hand either opening or closing, filmed from the angle at which one normally views ones own hands (see Figure 4). The left hand stimulus was created by flipping the right hand stimulus in a vertical axis. The warning stimulus occupied approximately 10.7° of visual angle horizontally and 16.4° vertically. The last frame of the opening stimulus movement occupied approximately 20.2° of visual angle horizontally and 16.7° vertically, whereas the last frame of the closing stimulus movement occupied approximately 10.6° horizontally and 15.1° vertically. As in Experiment 1, each movement consisted of 12 frames and lasted for 480ms.

Data recording and analysis were performed using the same method as in Experiment 1.

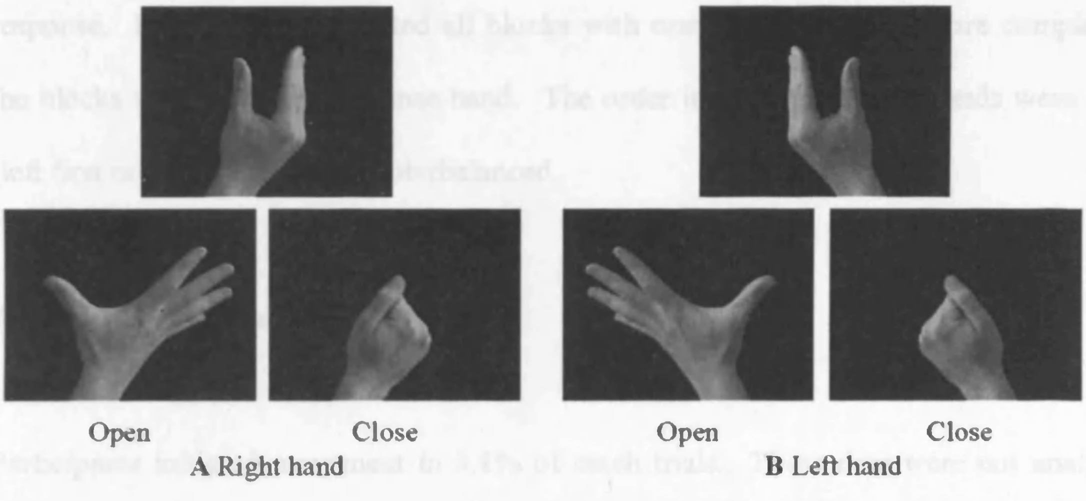


Figure 4: The stimuli used in Experiment 2, A Right hand, B Left hand. Within each stimulus type, the top image is the warning stimulus and the two images below are the last frame of the hand opening video (left) and the last frame of the hand closing video (right).

Procedure

The procedure was the same as that of Experiment 1 except as follows. First, the stimulus view variable (front or rear) in Experiment 1 was replaced with a stimulus identity variable (left or right hand). Second, responses were made in both left and right hemispaces. Given that participants were sitting with their response arm across their body, it was considered more comfortable that responses in left hemispace were made with the right hand (as in previous experiments), and responses in right hemispace were made with the left hand. This was not considered a likely confound for investigation of response hemispace because Cho & Proctor (2004) found that orthogonal spatial compatibility effects were not influenced by response hand. This experiment therefore contained twice as many blocks as Experiment 1; participants responded with their right hand in half the blocks, and their left hand in the other half. This resulted in four blocks in which closing was the required response and four in which opening was the required response. Participants completed all blocks with one response hand before completing the blocks with the other response hand. The order in which response hands were used (left first or right first) was counterbalanced.

2.2.2 Results and discussion

Participants initiated movement in 3.1% of catch trials. These data were not analysed further. Practice trials, incorrect response types (0.07%) and response omissions (0.20%) were excluded from the analysis. There were no RTs smaller than 100ms or greater than 1000ms. The RT data, shown in Figure 5, were subjected to ANOVA in which action compatibility (compatible and incompatible), stimulus hand identity (left or right) and response hemispace (left or right) were within-subject variables.

This analysis revealed a significant main effect of action compatibility (F(1,15) = 10.7, p = 0.005). On average, responding was 22ms faster when the stimulus and response action type were compatible (M = 362.8ms, SEM = 17.2 ms) than when they were incompatible (M = 385.2ms, SEM = 22.5ms). There was also a compatibility x response hemispace interaction, such that the compatibility effect was greater when participants responded in right hemispace (with the left hand) (29ms), than when they responded in left hemispace (with the right hand) (16ms) (F(1,15) = 5.8, p < 0.03). There was no evidence of a compatibility x stimulus hand interaction (F < 1).

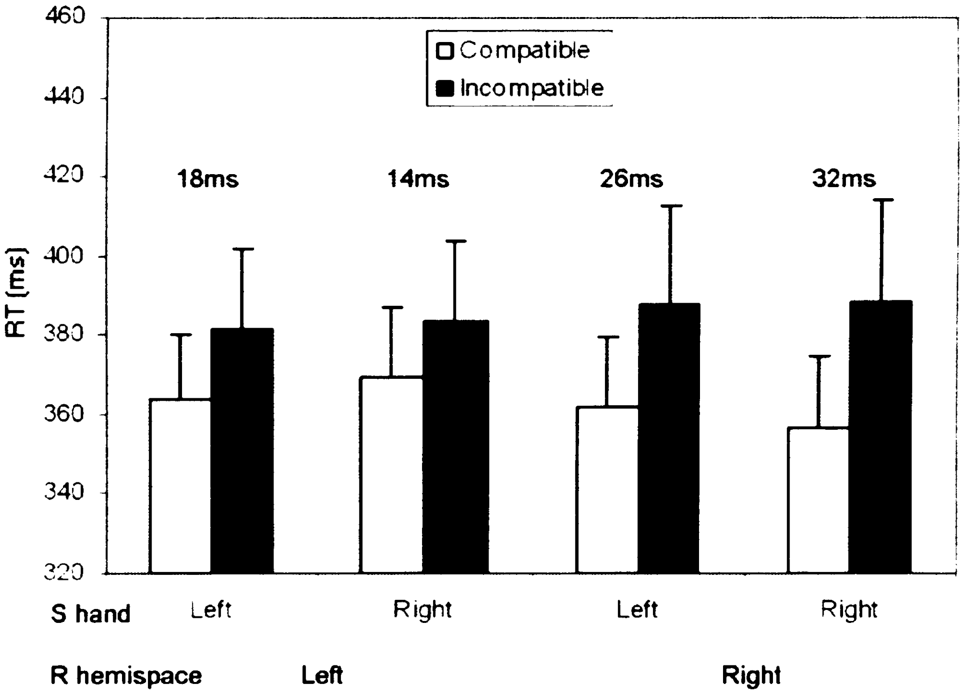


Figure 5: Experiment 2. Mean RT on action compatible (open bars) and incompatible (shaded bars) trials as a function of stimulus hand identity (left or right) and response hemispace (left or right). Vertical bars indicate the standard error of the mean and numbers indicate the magnitude of the compatibility effect.

There was a trend towards a compatibility x response hemispace x stimulus hand interaction; in right hemispace (responding with the left hand) the compatibility effect was greater with a right stimulus hand than with a left stimulus hand, and in left hemispace (responding with the right hand) the compatibility effect was greater with a left stimulus hand than with a right stimulus hand (see Figure 5). This interaction was not reliable ($F(1,15) = 2.1$, $p = 0.2$) but, owing to its theoretical significance, analyses were conducted to check whether there was a compatibility x stimulus hand interaction in either hemispace. These analyses demonstrated no evidence of such an interaction when participants responded in left hemispace ($F < 1$) or in right hemispace ($F(1,15) = 3.0$, $p = 0.1$).

Therefore, Experiment 2 provides evidence consistent with Experiment 1, suggesting that compatibility effects with opening and closing hand movements are driven by configural action compatibility rather than orthogonal spatial compatibility. Experiment 2 replicated the findings of Experiment 1 that compatibility effects are identical regardless of stimulus movement direction; responses (e.g. opening the hand) were faster when they were compatible with the stimulus action type (opening) than when they were incompatible (closing), regardless of stimulus movement direction (leftward or rightward). It provides more convincing evidence than Experiment 1 that movement direction does not contribute to compatibility effects because stimuli which moved in opposite directions when opening and closing had identical configural properties. Experiment 2 also did not detect any variations in compatibility effects in left and right hemispaces which may have been predicted if effects were mediated by orthogonal spatial compatibility.

2.3 General discussion

The experiments reported in this chapter addressed whether the compatibility effects observed with hand opening and closing movements result from configural action compatibility or orthogonal spatial compatibility. They have provided evidence to suggest that such compatibility effects result from configural action compatibility. Responses (e.g. hand opening) were faster when they were compatible with the stimulus configural action type (opening) rather than incompatible (closing), regardless of stimulus movement direction when opening and closing (fingers moving to the left or right).

The finding in Experiments 1 and 2 that the compatibility effects generated with opening and closing hand movements are driven by configural action compatibility is of importance for two reasons. First, these findings indicate that configural spatial codes contribute towards action compatibility, which is in line with findings of Brass et al. (2001). This procedure has made one improvement over and above that of Brass et al. (2001); this procedure has removed any influences of simple egocentric spatial compatibility, rather than arranging simple egocentric spatial compatibility in opposition to configural compatibility. This can potentially increase the sensitivity of the paradigm to configural compatibility and also, variations in compatibility effects can be attributed to variations in configural compatibility rather than simple egocentric compatibility.

The finding that configural compatibility contributes towards effects is consistent with neurological research which suggests that observed actions are encoded configurally in STS (e.g. Jellema & Perrett, 2006; Thompson et al., 2005; Jellema et al., 2000; Oram & Perrett, 1996; Perrett et al., 1991; Perrett et al., 1989; Perrett et al., 1985), and that cortical areas which are candidate neurological mechanisms of imitation encode actions configurally (Johansen-Berg et al., 2002; Schluter et al., 2001; Schluter et al., 1998; Gallese et al., 1996; Rizzolatti et al., 1996). If actions can be represented configurally in mechanisms mediating imitation, this may explain our ability to imitate actions when we are not aligned with the subject we are imitating.

Second, finding that these effects reflect configural action compatibility rather than orthogonal spatial compatibility indicates that the paradigm is appropriate for investigating imitation mechanisms in this thesis.

Chapter 3: Top-down and bottom-up contributions to the human imitative bias

Experiments reported in Chapter 2 have indicated that compatibility effects resulting from observing and executing hand opening and closing movements, where stimulus and response hands are in orthogonal dimensions, are driven by action compatibility. This chapter will therefore use these movements and the stimulus-response compatibility paradigm used in Experiments 1 and 2 to investigate whether the human imitative bias (Buccino et al., 2004; Tai et al., 2004; Castiello, 2003; Kilner et al., 2003; Castiello et al., 2002; Stevens et al., 2000; Abravanel & DeYong, 1991; Legerstee, 1991) emerges through top-down modulation of imitation mechanisms on the basis of knowledge about whether stimuli are human, or through perceptual properties of stimuli.

Imitation mechanisms have been implicated in a variety of higher sociocognitive functions, such as action understanding (Iacoboni et al., 2005; Rizzolatti, 2005), empathy (Carr, Iacoboni, Dubeau, Mazziota, & Lenzi, 2003; Gallese, 2003), theory of mind (Gallese & Goldman, 1998) and language (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziota, 2004; Rizzolatti & Arbib, 1998). For example, it has been proposed that we could understand an observed action by translating it into a motor representation which is active when we perform that action. Through activation of this motor representation, the intentions of an observed party could be inferred on the basis of what our intentions would have been if performing that action; we know when we execute the motor command to smile that a possible intention could be to convey happiness or appreciation. This theory of mental state understanding has led some to hypothesise that deficient imitation mechanisms underlie the reduced capacity for these aspects of social cognition in developmental disorders such as autism (Williams et al., 2006; Williams, Whiten, Suddendorf, & Perrett, 2001).

These higher sociocognitive functions may depend, not only on the transmission of information from imitation mechanisms to higher level sociocognitive mechanisms, but also on top-down modulation of imitation mechanisms *from* these higher level mechanisms (Nishitani, Avikainen, & Hari, 2004). It would be ineffective to make higher-level social inferences from most non-human stimuli (excluding other animals) because it is generally assumed that these non-human systems do not have mental states. Therefore, on the basis of knowledge about whether social inferences can be made from a stimulus, higher-level mechanisms may gate operation of imitation mechanisms. This may be achieved if, as suggested by Castielli, Frith, Happe, & Frith (2002), the temporal pole and/or medial prefrontal cortex modulate activity in the STS (Allison, Puce, & McCarthy, 2000) on the basis of whether stimuli are or are not social. This process could influence the operation of imitation mechanisms through the many connections between STS and premotor cortex via the rostral part of the inferior parietal lobule (Rizzolatti, 2005).

There is no evidence to date that the human imitative bias is due to top-down modulation of imitation mechanisms on the basis of knowledge about stimulus identity. However, Grezes et al. (1998) have found another top-down influence on imitation mechanisms. They found greater activation in premotor cortex and superior parietal lobule when participants observed an action in order to imitate it later than when they observed an action without any specific purpose. Therefore, the operation of imitation mechanisms may not depend only on the specific stimuli presented, but also on knowledge of possible future tasks to be performed in relation to those stimuli.

Alternatively or additionally, the human imitative bias may be driven by perceptual properties of the stimuli. Regardless of beliefs about stimulus identity, a human stimulus may be more readily imitated than a non-human stimulus. The human imitative bias may be driven directly by features of the stimulus movement such as shape or colour, or by the spatiotemporal dynamics of the movement (e.g. Bonda, Petrides, Ostry, & Evans, 1996).

To investigate the top-down and bottom-up contributions to the human imitative bias in automatic imitation, Experiments 3 and 4 assessed the impact of stimulus variables and of beliefs on automatic imitation of human and robotic hand movements. Like Experiments 1 and 2, participants were required to make a pre-specified response (open or close their hand) whenever they detected an observed stimulus hand start to move (open or close). In Experiment 3, the moving parts of the human and robotic stimuli were identical (human), while participants' instructions about their identity (human or robotic) were varied. Silhouette stimuli were used to make it more likely that participants would believe in one condition that stimuli were robotic; there were no fine aesthetic details of skin or shading which might appear difficult to manufacture. In Experiment 4, one group of participants observed genuinely human movements like those used in Experiment 3, and the other group observed more angular and symmetrical movements of a non-human hand. Like Experiment 3, instructions about identity (human or robotic) were varied. In Experiments 3 and 4, an effect of instruction would indicate top-down influence, and in Experiment 4, an effect of genuine stimulus type would indicate bottom-up influence.

3.1 Experiment 3

All participants in Experiment 3 participated in two sessions of testing; prior to one session they were instructed that the stimuli were human, and prior to the other that they were robotic. In reality, the moving parts of all stimuli were human silhouette stimuli. Silhouettes were a bright blue colour to ensure high contrast with the black background, making movements easily detectable.

If the human imitative bias is mediated by top-down influence on imitation mechanisms on the basis of belief about stimulus identity, stimuli which participants were instructed were human should evoke greater automatic imitation than stimuli which participants were instructed were robotic. However, if beliefs about identity do not contribute towards the human imitative bias, one would expect automatic imitation of the stimuli to be identical under the two instruction conditions.

3.1.1 Method

Participants

Thirteen consenting, healthy volunteers with an average age of 22.9 years, five male, participated in Experiment 3, and were paid a small honorarium for their participation. The data from one participant was removed from the analysis because less than 90% of their data was remaining following employment of the various exclusion criteria.

Stimuli

Stimuli were presented using the same apparatus as in Experiments 1 and 2. The stimuli were two movements (opening and closing) made by a blue silhouette of a human right hand, with either a human naturalistic wrist ('human' stimuli) or a wrist made from steel rods and wire ('robotic' stimuli). Wrists which distinguished the identity of the stimuli were thought to increase the likelihood that participants would remember the information about stimulus identity supplied by the experimenter at the beginning of the experiment. The two stimulus types ('human' and 'robotic') are shown in Figure 6. Both human movements were filmed from the angle at which one normally views ones own hands, and began with the fingers closed and pointing upwards in parallel with the thumb (warning stimulus). The warning stimulus occupied approximately 10.7° of visual angle horizontally and 16.4° vertically. In the opening movement, the fingers and thumb splayed, and, in the closing movement, they rolled into a fist. The final open posture

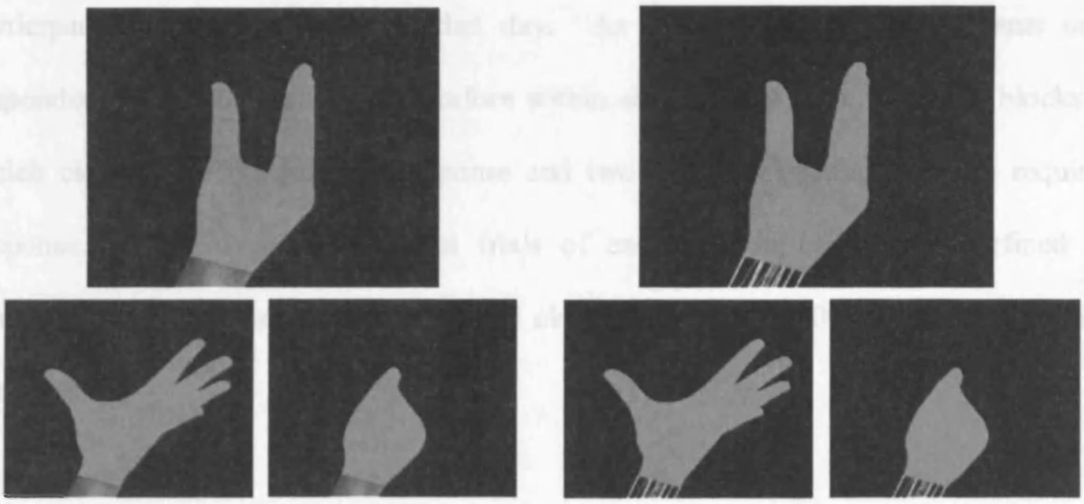


Figure 6: The stimuli used in Experiment 3, A 'Human' hand, B 'Robotic' hand. Within each stimulus type, the top image is the warning stimulus and the two images below are the last frame of the hand opening video (left) and the last frame of the hand closing video (right).

occupied approximately 20.2° of visual angle horizontally and 16.7° vertically, whereas the final close posture occupied approximately 10.6° horizontally and 15.1° vertically. Each movement consisted of 12 frames and had a duration of 480ms. The hands appeared approximately life-sized.

Data recording and analysis were performed using the same method as in Experiments 1 and 2.

Procedure

The procedure was the same as that of Experiments 1 and 2 except as follows. Each participant completed two sessions of testing. Participants were instructed that the stimuli were human prior to one session of testing, and robotic prior to the other. The instructions were not elaborate; it was simply stated 'you will observe a human / robotic hand making opening and closing movements', according to the stimulus type which the participant would be viewing on that day. As in Experiment 1, participants only responded with their right hand, therefore within each session there were two blocks in which closing was the required response and two in which opening was the required response. There were ten stimulus trials of each type in each block, defined by combination of the stimulus (opening and closing) and SOA (800, 1600, and 2400ms) variables.

Following the completion of the simple RT task in each session, participants were given a 14-item questionnaire assessing their beliefs about the animacy of the stimulus observed (see Figure 7). The first nine questions assessed beliefs about animacy directly. For example, 'Did the movement seem to be active or passive?' Questions 10-14 assessed beliefs indirectly by asking how participants would feel about interacting with the stimulus. For example, 'How would you feel about the hand assisting in surgery on your body?'. Each question was presented on a separate response screen, and was answered before viewing the next question. Responses were registered by movement of a vertical scroll-bar located below each question. The lower end of each scroll-bar was labelled with a minimally animate response to that question, for example, the lower end in question 3 was labelled 'passive'. The higher end of each scroll-bar was labelled with a maximally animate response to that question, for example, the higher end in question 3 was labelled 'active'. A score out of 50 was derived from the answer to each question, with a response at the maximally lower end of the scroll-bar scoring 0 and a response at the maximally higher end of the scroll-bar scoring 50.

1. How purposeful and goal-directed did the movement appear?
2. Did the image appear to be moving by itself or did it seem to be driven by something else?
3. Did the movement seem to be active or passive?
4. How natural were the movements?
5. How human did the movement appear?
6. How male do you think this movement was?
7. How female do you think this movement was?
8. How vigorous do you feel the movement was?
9. If the hand was cut, would it feel pain?
10. How would you have felt if this hand had reached out and grasped your hand?
11. How would you have felt if this hand had waved at you?
12. How would you feel about the hand combing your hair?
13. How would you feel about the hand touching your eyelids?
14. How would you feel about the hand assisting in surgery on your body?

Figure 7: Questionnaire questions in Experiment 3.

Participants returned for the second session of testing, not less than one day later and not more than one week later. For each participant, the order of responses to be made (opening their hand or closing their hand first) was constant across the first and second days of testing. The order in which responses were tested (open first or close first), and the order of belief manipulation (instructed that the stimulus hand was human or robotic first) were counterbalanced.

3.1.2 Results and discussion

ANOVA was applied to the questionnaire data in which instruction about stimulus type (human and robotic) was a within-subject variable. This analysis indicated that animacy ratings (an average of questions 1-14) were higher for stimuli which participants were instructed were human (M = 28.3/50, SEM = 1.9) than for stimuli which they were instructed were robotic (M = 23.5/50, SEM = 1.5) (F(1,11) = 12.1, $p < 0.01$), and this effect did not interact with any of the counterbalancing variables. This suggests that the instructions were effective in influencing participants' beliefs about the objects depicted in the stimulus images. The effect of instruction on animacy ratings was small, but highly reliable. It is likely that the effect was small because participants were reluctant to use the extremes of the rating scale.

Participants initiated movement in 10.1% of catch trials. These data were not analysed further. Practice trials and all RTs smaller than 100ms and greater than 1000ms (0.24%) were excluded from the analysis. There were no incorrect response types or response omissions. The RT data are shown in Figure 8 and were subjected to ANOVA in which compatibility (compatible and incompatible) and instruction about stimulus type (human and robotic) were within-subject variables. This analysis revealed a main effect of compatibility (F(1,11) = 32.0, $p < 0.001$). On average, responding was 20ms faster when the stimulus was response-compatible (M = 361.8ms, SEM = 11.1ms) than when it was response-incompatible (M = 382.5ms, SEM = 13.4ms). This RT difference was *not* greater for stimuli which participants were instructed were human. In fact, as Figure 8 indicates, the RT difference was numerically greater for stimuli which participants were instructed were robotic, but this difference was not reliable (F(1,11) = 1.8, p = 0.2), nor did it interact with any of the counterbalancing variables. Figure 8 also indicates faster responding to stimuli which participants were instructed were robotic than to stimuli which participants were instructed were human, but this difference was only marginally significant (F(1,11) = 4.7, p = 0.05). No other effects or interactions were significant.

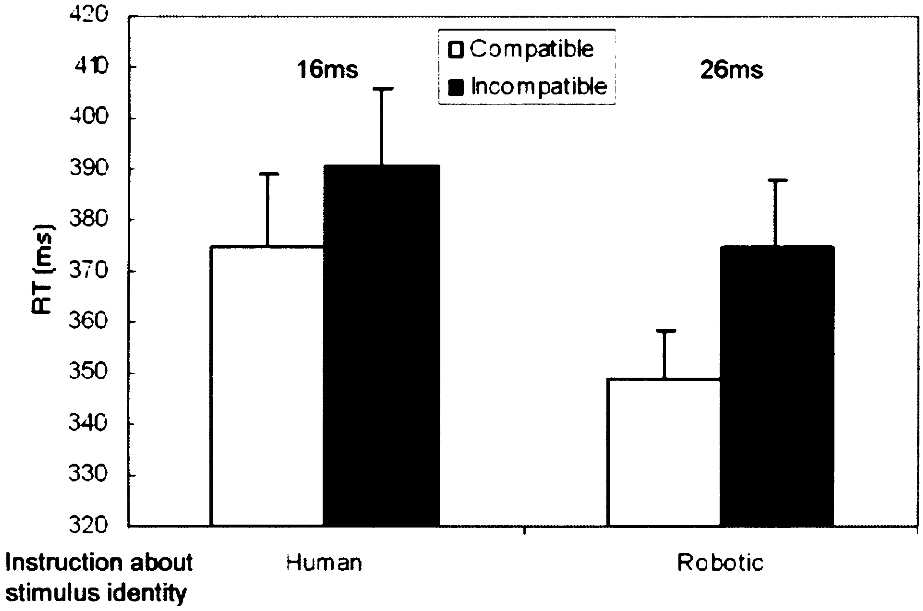


Figure 8: Experiment 3. Mean RT on compatible (open bars) and incompatible (shaded bars) trials for stimuli which participants were instructed were human and stimuli which participants were instructed were robotic. Vertical bars indicate the standard error of the mean and numbers indicate the magnitude of the compatibility effect.

Therefore, Experiment 3 did not detect any top-down influence of beliefs about stimulus identity on automatic imitation. Despite questionnaire responses indicating that the instructions successfully manipulated the participants' beliefs about stimulus identity, automatic imitation of stimuli which participants were instructed were human was not greater than automatic imitation of stimuli which participants were instructed were robotic.

3.2 Experiment 4

Although Experiment 3 found no influence of instruction about stimulus identity on automatic imitation, the instruction manipulation in Experiment 3 was confounded with a minor perceptual variable. The stimuli which participants were instructed were human had a human naturalistic wrist, and the stimuli which participants were instructed were robotic had a wrist made from steel rods and wires. This perceptual modulation was employed because it was thought to increase the probability that participants would remember their instructions about stimulus identity during the experiment. However, this perceptual modulation may have masked an effect of instruction on automatic imitation. For example, there was a trend for participants to respond more slowly to stimuli which they had been instructed were human, and also for these stimuli to elicit less automatic imitation. Slower responses to human stimuli may have resulted if the human wrists captured greater attention than the robotic wrists, therefore resulting in less attention towards the moving parts of the stimulus. Given that these experiments employ a simple RT procedure, participants may have responded to slight movement observable near the wrist, rather than the entire movement which would have been processed if focussing attention further upwards. If this perceptual difference had not been present, greater automatic imitation of stimuli which participants were instructed were human may have been observed. Experiment 4 therefore provided a further test of the top-down hypothesis, where the stimuli which participants were instructed were human were identical to the stimuli which participants were instructed were robotic.

In addition to providing a further test of the top-down hypothesis, Experiment 4 investigated any bottom-up contribution to the human imitative bias. Genuine stimulus identity was manipulated in addition to beliefs about stimulus identity. One group of participants always observed human movements, and prior to one session they were instructed that the movements were human and prior to the other session that they were robotic. These genuinely human stimuli were the same as those presented in Experiment 3, but were now identical irrespective of whether participants were instructed that they were human or robotic, that is, they did not have discriminating wrists. The other group observed more angular and symmetrical movements of a non-human hand, and prior to one session they were instructed that the movements were generated by a human agent and prior to the other session that they were generated by a robotic agent. These genuinely non-human movements were created by approximately matching each frame of the opening and closing movements to each frame of the opening and closing human movements in surface area, luminance, horizontal and vertical visual angles, and aperture between closest effectors. These genuinely non-human movements were created to appear robotic by making them angular and symmetric, in contrast to the human movements which were asymmetric with rounded contours. Although these movements were not in fact generated by a mechanically-driven device, they will be termed 'genuinely robotic' in this chapter, in order to distinguish them from the stimuli which were genuinely human.

If there are bottom-up contributions to the human imitative bias, then genuinely human movements should evoke a larger automatic imitation effect than genuinely robotic movements. If there are top-down contributions, then stimuli believed to be human should evoke a larger automatic imitation effect than stimuli believed to be robotic.

3.2.1 Method

Participants

Twenty-five new, consenting, healthy volunteers with an average age of 25.2 years, seven male, participated in Experiment 4, and were paid a small honorarium for their participation. The data from one participant was removed from the analysis because less than 90% of their data was remaining following employment of the various exclusion criteria. The remaining 24 participants were randomly assigned in equal numbers to groups which viewed a genuinely human stimulus, or a genuinely robotic stimulus, across both days of testing.

Stimuli

The two stimulus types (human and robotic) are shown in Figure 9. The group observing genuinely human movements in both sessions of testing received the same instructions about identity as the participants in Experiment 3; the participants were simply instructed that the movements were either human or robotic. The participants presented with the genuinely robotic stimuli were instructed that the movements were generated by either human or robotic movement, through taking important points of motion and mapping these onto a stimulus "in a similar way to that in which they make characters move in films like Shrek©". It was thought that these instructions were more believable than instructing participants that the angular form of the stimuli was human.

All other aspects of the method were the same as in Experiment 3.

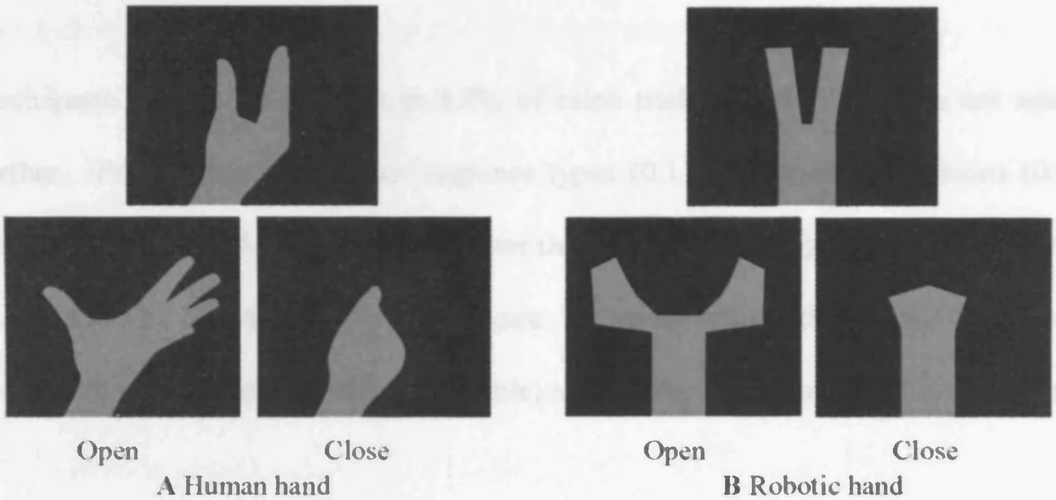


Figure 9: The stimuli used in Experiment 4, A Human hand, B Robotic hand. Within each stimulus type, the image on the left is the last frame of the hand opening video and the image on the right is the last frame of the hand closing video.

3.2.2 Results and discussion

ANOVA was applied to the questionnaire data in which instruction about stimulus type (human and robotic) was a within-subject variable and genuine stimulus type (human and robotic) was a between-subject variable. This ANOVA indicated that animacy ratings (an average of questions 1-14) were higher for stimuli which participants had been instructed were human (M = 24.1/50, SEM = 1.0) than for stimuli which they had been instructed were robotic (M = 21.2/50, SEM = 0.9) (F(1,22) = 17.0, $p < 0.001$), and this effect did not interact with any of the counterbalancing variables. This suggests that, as in Experiment 3, the instructions were effective in manipulating participants' beliefs about stimulus type. The ratings for genuinely human stimuli (M = 23.9/50, SEM = 1.4) and genuinely robotic stimuli (M = 21.3/50, SEM = 1.0) did not reliably differ (F(1,22) = 2.3, p = 0.1), which is perhaps surprising. This similarity in ratings for genuinely human and robotic stimuli may indicate that the instructions regarding stimulus origin were so effective that they blocked any effects of stimulus properties on beliefs.

Participants initiated movement in 4.8% of catch trials. These data were not analysed further. Practice trials, incorrect response types (0.11%), response omissions (0.05%) and all RTs smaller than 100ms and greater than 1000ms (0.03%) were excluded from the analysis. The RT data, shown in Figure 10, were subjected to ANOVA in which compatibility (compatible and incompatible) and instruction about stimulus type (human

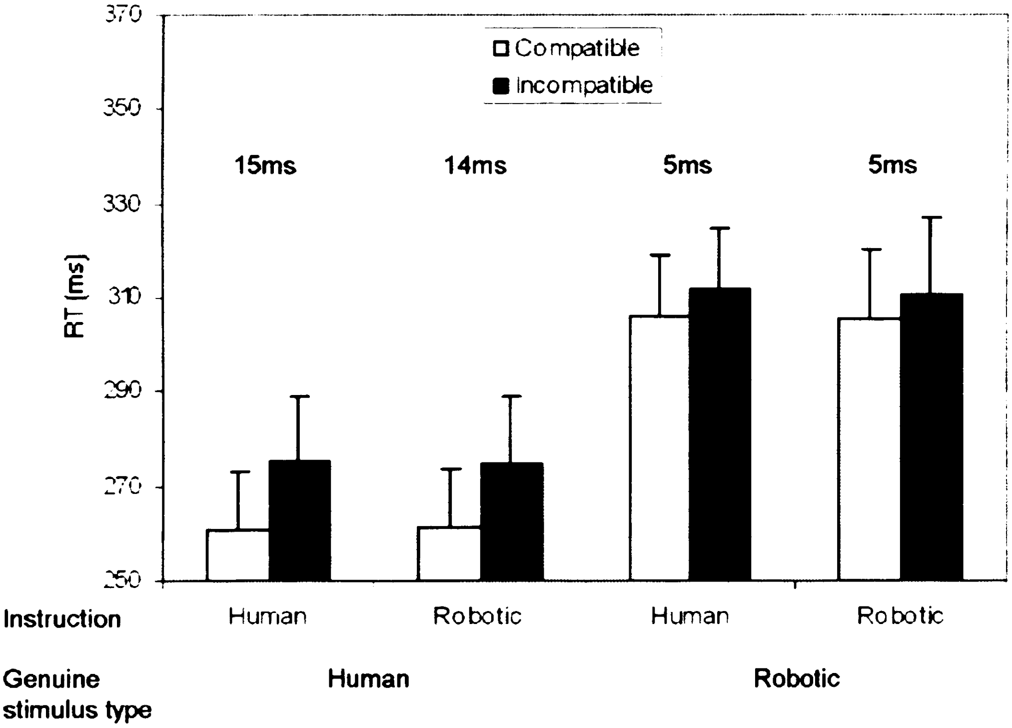


Figure 10: Experiment 4. Mean RT on compatible (open bars) and incompatible (shaded bars) trials for genuine human (left) and robotic (right) stimuli, both when instructed to be human and when instructed to be robotic. Vertical bars indicate the standard error of the mean and numbers indicate the magnitude of the compatibility effect.

and robotic) were within-subject variables and genuine stimulus type (human and robotic) was a between-subject variable. There was a main effect of compatibility ($F(1,22) = 20.7$, $p < 0.001$), and a genuine stimulus type x compatibility interaction ($F(1,22) = 4.5$, $p < 0.05$). On average, responding was 10ms faster when the stimulus movement was response-compatible (M = 283.5ms, SEM = 8.8ms) than when it was response-incompatible (M = 293.1ms, SEM = 9.8ms), and this difference was greater for participants who responded to genuinely human stimuli (14.2ms) than for participants who responded to genuinely robotic stimuli (5.2ms). Simple effects analyses indicated that the difference in RT between compatible and incompatible trials was significant, not only for genuinely human stimuli ($F(1,11) = 13.7$, $p < 0.005$), but also for genuinely robotic stimuli ($F(1,11) = 8.0$, $p < 0.02$). As in Experiment 3, the instruction x compatibility interaction was not significant ($F < 1$), and this did not interact with any of the counterbalancing variables.

There was also a main effect of genuine stimulus type ($F(1,22) = 4.8$, $p < 0.05$), indicating that, on average, participants observing genuinely human stimuli were faster to respond (M = 268.1ms, SEM = 12.4ms) than participants observing genuinely robotic stimuli (M = 308.5ms, SEM = 13.7ms). This suggests that it may have taken participants longer to process movement features of the robotic stimuli than movement features of the human stimuli. Some supplementary analyses were performed to investigate whether the main effect of genuine stimulus type could have created the genuine stimulus type x compatibility interaction. Investigations of simple spatial compatibility have indicated that faster responses are associated with larger compatibility effects (Eimer, Hommel, & Prinz, 1995; De Jong, Liang, & Lauber, 1994; Hommel, 1993), and this finding is thought to reflect decay in the representation of the visual stimulus over time, after its initial activation following presentation. If this is the case with the stimuli used in Experiment 4, the main effect of genuine stimulus type could have created the genuine stimulus type x compatibility interaction; by the time the participants respond to the genuinely robotic stimulus, the representation of the visual stimulus will have decayed relative to the time at which participants respond to the genuinely human stimulus.

The RT distribution for each participant within Experiment 4 was therefore divided into quintiles (Ratcliff, 1979). Compatibility effects could therefore be compared for five levels of response speed; quintile 1 indicating the fastest trials of each type and quintile 5 indicating the slowest. An ANOVA was performed on these data in which compatibility (compatible and incompatible), belief about stimulus type (human and robotic) and response speed (quintiles 1, 2, 3, 4 and 5) were within-subject variables and genuine stimulus type (human and robotic) was a between-subject variable. This analysis demonstrated that compatibility effects increased as RT increased, although this effect was not quite reliable ($F(4,88) = 3.6$, $p = 0.06$, Greenhouse Geisser corrected). This effect did not differ as a function of genuine stimulus type ($F(4,88) = 2.0$, $p = 0.2$). This finding is in line with previous investigations of configural action compatibility, where compatibility effects have been found to increase with increasing RT (Bird, 2003; Brass et al., 2001). This may be because configural spatial features of action take longer to process than simple spatial features and therefore become more active over time.

This analysis indicates that larger compatibility effects should be expected, in principle, at slower RTs, therefore the main effect of genuine stimulus type is unlikely to have created the genuine stimulus type x compatibility interaction. However, these analyses were performed within-subject. An additional analysis was performed to note whether these effects were also present between-subject. All participants from Experiments 1 – 4 were included in this analysis. There was a reliable correlation between mean RT and mean compatibility effect (Pearson's $r = 0.66$, $p < 0.001$); as mean RT increased, so did mean compatibility effect. This analysis provides further evidence to suggest that it is unlikely that the main effect of genuine stimulus type has created the genuine stimulus type x compatibility interaction, and that it is more likely that the main effect diluted the interaction such that a larger interaction would have been observed in its absence.

Like those of Experiment 3, the results of Experiment 4 therefore provide no support for the hypothesis that beliefs about stimulus identity play a significant role in mediating the human imitative bias. There were no perceptual differences between stimuli which participants were instructed were human and those which they were instructed were robotic. This eliminates the possibility that perceptual differences were masking influences of belief. In contrast, the results of Experiment 4 indicate that stimulus properties can contribute to the human imitative bias.

3.3 General discussion

To investigate bottom-up and top-down contributions to the human imitative bias, Experiments 3 and 4 assessed the impact of stimulus variables and of instructions about stimulus identity on automatic imitation of human and robotic hand movements. In Experiment 3, the moving parts of the stimuli were human, but participants were instructed prior to one session that the stimuli were human and prior to another session that the stimuli were robotic. Experiment 3 found no evidence that beliefs about stimulus identity exert a top-down influence on automatic imitation; there was not a larger automatic imitation effect elicited by the human movements when participants were instructed that they were human than when they were instructed that they were robotic. Experiment 4 replicated this finding and also indicated that, rather than beliefs about stimulus identity, properties of the movement stimuli influence automatic imitation. In a factorial design, participants were presented with stimuli which were genuinely human or genuinely robotic, and were instructed prior to one session that the stimuli were human and prior to another session that the stimuli were robotic. This experiment found that automatic imitation of genuinely human stimuli was greater than automatic imitation of genuinely robotic stimuli, but did not find evidence that this difference was modulated by beliefs about the human or robotic origin of the stimuli.

As discussed in Chapter 1, previous behavioural studies have shown that observation of human movements elicits more automatic imitation than observation of robotic movements (e.g. Oztop et al., 2004; Kilner et al., 2003). Neurological studies have also suggested a human visuomotor priming advantage, by showing that observation of human movements gives rise to more activity in premotor cortex than observation of robotic movements (Tai et al., 2004). However, as far as I am aware, no previous study has attempted to isolate and distinguish top-down and bottom-up contributions to the human imitative bias.

It has been suggested that imitation mechanisms influence higher sociocognitive functions via connections with higher level mechanisms involved in drawing inferences about mental states (Rizzolatti, 2005; Kilner et al., 2003; Gallese & Goldman, 1998). The finding that the human imitative bias depends on stimulus properties rather than beliefs about stimulus origin is not inconsistent with this suggestion. It is generally assumed that humans and other animals have mental states whereas robotic systems do not. Therefore, it would be adaptive for inputs from biological stimuli to have privileged access to processes which generate inferences about mental states. Although the present results are consistent with the hypothesis that imitation mechanisms provide input to higher-level sociocognitive functions, they provide no support for the converse hypothesis, that higher-level functions modulate processing in imitation mechanisms.

The observation that the human imitative bias is driven by stimulus properties rather than beliefs about stimulus origin is consistent with both AIM and ASL theories of imitation. The AIM model proposes that imitation mechanisms evolved through natural selection, and Meltzoff & Decety (p.491, 2003) suggest that imitation may have evolved to support social understanding: 'nature endows humans with the tools to solve the 'other minds' problem by providing newborns with an imitative brain'. Other authors have made similar suggestions that imitation evolved for such social understanding (Kilner et al., 2003; Gallese & Goldman, 1998). This hypothesis may predict that imitation mechanisms therefore allow privileged access to human stimuli. The ASL theory of imitation is also consistent with a human imitative bias mediated by stimulus properties. Our environment provides us with many opportunities to form associations between visual representations of human movements and matching motor representations. For example, automatic imitation of hand movements may depend on links established during visual observation of ones own hand whilst performing movements. In comparison, there would be relatively little opportunity to form similar associations between visual representations of robotic movements and motor representations of our own movements.

It might be argued that beliefs about stimulus origin do exert a top-down influence on imitation mechanisms, and that Experiments 3 and 4 did not detect such an influence because they did not effectively manipulate participants' beliefs about stimulus identity. A questionnaire was used to assess participants' beliefs about stimulus identity in Experiments 3 and 4 and questionnaire responses are susceptible to demand effects. In principle, participants may have responded in accordance, not with their beliefs about the objects depicted in the stimulus images, but with inferences about the experimenter's expectations. However, it is unlikely that our questionnaire measure was contaminated by demand effects for two reasons. First, the experimenter conspicuously did not observe participants when they were completing the questionnaire, and they were assured that all data would be stored anonymously. Second, questionnaire responses were made using a scroll-bar which was not marked with numbers. Therefore, it would have been difficult for participants to remember when completing the questionnaire after their second session (e.g. robot instructions) how they had responded after their first (e.g. human instructions), at least 24 hours earlier.

The results of Experiment 4 provide some information about the perceptual properties which can mediate the human imitative bias. Genuinely human and robotic stimuli differed only in shape; according to the terminology established in Chapter 2, the configural spatial properties differed. The stimuli did not differ in colour, texture, shading or overall size. This provides further support for the hypothesis that action compatibility is, at least partly, determined by compatibility between stimuli and responses on spatial coordinates (see Chapter 2). This is not to suggest that other features of stimuli do not influence automatic imitation. The ASL model would suggest that any perceptible feature of a stimulus can become associated with a response. This issue is discussed further in Chapters 4 and 6.

Experiment 4 indicated that, although less effective than human stimuli, robotic stimuli do elicit automatic imitation. This finding is in contrast to those of previous studies which have found no evidence of imitation of robotic stimuli (Castiello, 2003; Kilner et al., 2003; Castiello et al., 2002; Abravanel & DeYong, 1991; Legerstee, 1991) and no activation in motor circuits during observation of robotic movement (Tai et al., 2004). There are at least two possible reasons why the present study found evidence of imitation of robotic stimuli whereas previous studies did not (cf. Oztop et al., 2004). First, the robotic movement stimuli in Experiment 4 may have been more similar in appearance to human movement stimuli. Greater similarity of robotic and human stimuli may have elicited greater automatic imitation of robotic stimuli through stimulus generalisation from human stimuli (e.g. Pearce, 1987), that is, according to the ASL model, those features which are common to human and robotic movement will be associated with matching responses through learning with human stimuli. Experiment 4 certainly sought to achieve similarity between the human and robotic stimuli by matching the robotic to the human stimuli on several dimensions (e.g. surface area, horizontal and vertical visual angles, aperture between closest effectors), but without more detailed information about the stimuli used in previous experiments it is difficult to make the relevant cross-experimental comparisons. Second, in comparison with the behavioural and neurophysiological measures used in previous studies, the automatic imitation compatibility paradigm with hand opening and closing movements may be especially sensitive to imitation, and therefore able to detect even small tendencies to imitate robotic stimuli.

Conclusion: The experiments reported in this chapter provide no evidence that the human imitative bias is modulated by beliefs about whether observed stimuli are human or robotic. In contrast, the present findings indicate that the greater potency of human stimuli in eliciting imitation depends on visual properties of the stimuli; that the human imitative bias is predominantly a bottom-up, rather than a top-down, effect.

Chapter 4: The role of experience in imitation of non-human stimuli

The experiments reported in Chapter 3 suggest that the human imitative bias is driven by perceptual properties of the stimuli. This is consistent with both AIM and ASL models of imitation. However, the AIM and ASL models make different predictions concerning whether imitation of stimuli can be modulated by training and hence, whether the bias can be modulated by training. The ASL model predicts that a stimulus-driven human imitative bias results from greater opportunity for associative learning connecting visual representations of human movement with matching motor representations, relative to similar opportunities with non-human visual representations of movement. Therefore, training where participants are required to perform responses which are compatible with the movements of non-human stimuli (compatible training) should lead to greater imitation of those stimuli, relative to training where participants are required to perform responses which are incompatible with the movements of non-human stimuli (incompatible training). This hypothesis therefore predicts that the human imitative bias can be modified. In contrast, the AIM model assumes that a stimulus-driven human imitative bias is mediated by innate structures, and therefore predicts that training with non-human stimuli should have little influence on imitation of these stimuli and that the human imitative bias cannot be modified.

The experiments reported in this chapter aimed to distinguish AIM and ASL theories of a human imitative bias by testing for effects of compatible and incompatible training with robotic stimuli on automatic imitation of those stimuli, and hence, the human imitative bias. The purpose of Experiment 5 was to establish a human imitative bias with human and robotic stimuli which were more suitable for use in training paradigms than the stimuli used in Experiment 4. Experiments 6 and 7 addressed whether compatible training with robotic stimuli would result in greater automatic imitation of those stimuli relative to incompatible training. In both training groups, automatic imitation with robotic stimuli was established at pre-test sessions, and compared against automatic imitation at post-test sessions. Comparisons between compatible and incompatible training groups enabled isolation of those effects of associative learning, relative to those of perceptual learning with robotic stimuli (e.g. Chamizo & Mackintosh, 1989; Gibson, 1969) and response practice. Imitation of robotic stimuli was compared against imitation of human stimuli to establish whether training modulated the human imitative bias. The AIM model would predict that training should have no systematic influence on imitation of robotic stimuli, and hence, that the human imitative bias should not be modified. In contrast, the ASL model would predict that automatic imitation of robotic stimuli should be greater following compatible training with those stimuli relative to incompatible training. This hypothesis therefore predicts that the human imitative bias will decrease from pre- to post-test with compatible training, relative to incompatible training.

Experiment 6 employed a training procedure where participants were explicitly instructed to execute responses which were compatible or incompatible with observed stimulus movements. Experiment 7 employed a training paradigm which was similar to Experiment 6, but removed any reference to the stimulus-response relationship from instructions given prior to training. This was to investigate whether any influences of training observed in Experiment 6 reflected formation of long-term associations, established through practice and postulated by the ASL model to mediate imitation, or formation of short-term associations, established on the basis of task instructions given prior to training.

4.1 Experiment 5

Experiment 5 was designed to establish a human imitative bias with stimuli which were more suitable for use in training paradigms than the stimuli used in Experiment 4. To test for effects of training on automatic imitation of robotic stimuli and the human imitative bias, it was important to demonstrate that robotic stimuli elicited less automatic imitation than their human counterparts.

Experiment 5 implemented three changes relative to Experiment 4. First, Experiment 4 used moving stimuli to investigate automatic imitation, but Experiment 5 used terminal postures. Several authors have found that terminal postures are as effective, if not more effective, than movements in eliciting automatic imitation (Vogt et al., 2003; Craighero et al., 2002; Stürmer et al., 2000). Stürmer et al. (2000) reasoned that posture stimuli may have evoked larger automatic imitation effects because all participants responded to a fully-opened or fully-closed hand. With moving stimuli, fast participants will respond to stimuli which are not fully opened or closed. This reasoning means that in addition to larger average automatic imitation effects, posture stimuli may lead to a reduction in between-subject variability because all participants will respond to the same action stimuli. Because Experiments 6 and 7 were designed to compare effects of training between participants receiving different types of training (compatible and incompatible), these between-subject comparisons were likely to be clearer if there was less variation in initial levels of automatic imitation.

Second, the SOA between presentation of the warning stimulus and the imperative stimulus posture was made shorter, on average, and more variable than in Experiment 4.

Previous investigations have indicated that larger automatic imitation effects may be obtained with shorter average SOAs (Bird, 2003; Vogt et al., 2003; Stürmer et al., 2000), which may be driven by longer RTs at shorter SOAs (Niemi & Näätänen, 1981). More variable SOAs have also been found to increase RT (Niemi & Näätänen, 1981) which may also lead to larger automatic imitation effects. Increase in the magnitude of the automatic imitation effects detectable in these experiments may increase the probability of detecting a training effect (Howell, 1997).

Third, the experiments reported in this chapter did not require manipulation of beliefs about identity, and therefore it was possible to use stimuli which differed on a greater number of perceptual dimensions than the stimuli in Experiment 4, specifically, colour, texture and shading. To increase the generality of any findings, a human imitative bias was explored with two stimulus sets. The first set, 'schematic' stimuli, were bright blue silhouettes similar to those used in Experiment 4, therefore the human and robotic stimuli did not differ in colour, texture and shading. The human stimuli were silhouettes of a human hand, and the robotic stimuli were created by approximately matching each stimulus to the corresponding human stimulus in surface area, luminance, horizontal and vertical visual angles, and aperture between closest effectors. As in Experiment 4, stimuli were made to appear robotic by making them angular and symmetric. The second set, 'naturalistic' stimuli, differed on a greater number of perceptual dimensions. Human naturalistic stimuli were photographs of a human hand; these stimuli were therefore flesh colour with shading defining the smoothly rounded effector parts. Robotic naturalistic stimuli were photographs of a mechanical claw; these stimuli were therefore metallic in colour, with shading defining the angular parts.

Thus, Experiment 5 established levels of automatic imitation with human naturalistic, human schematic, robotic naturalistic and robotic schematic posture stimuli. It was expected that human stimuli would elicit larger automatic imitation effects than robotic stimuli, as in Experiment 4, and that these stimuli could be used in Experiments 6 and 7 to investigate the effects of training with robotic stimuli on automatic imitation of robotic stimuli and the human imitative bias.

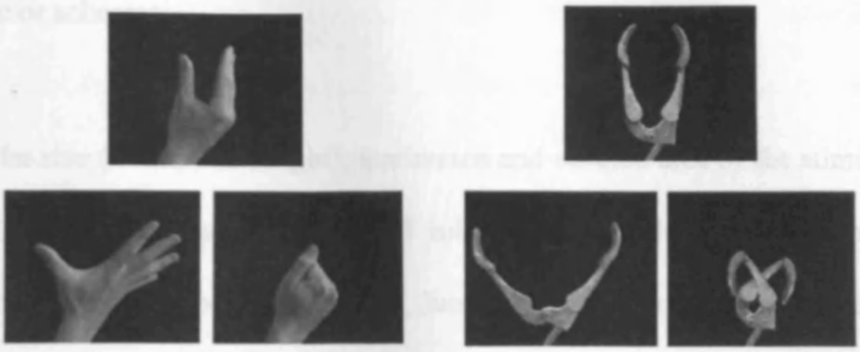
4.1.1 Method

Participants

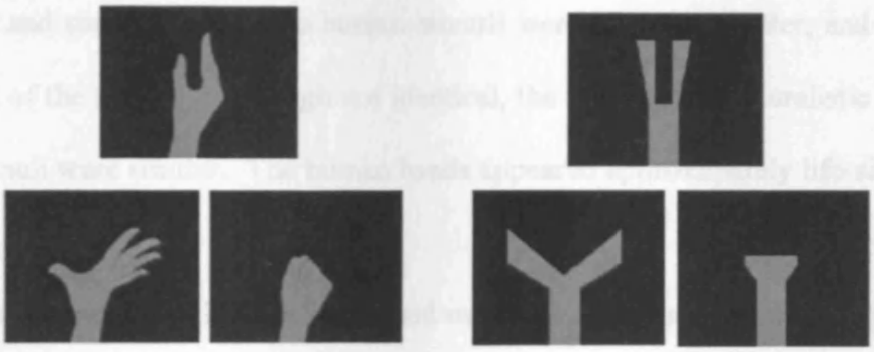
Seventeen consenting, healthy volunteers with an average age of 25.6 years, seven male, participated in Experiment 5, and were paid a small honorarium for their participation. The data from one participant was removed from the analysis because less than 90% of their data was remaining following employment of the various exclusion criteria.

Stimuli

Stimuli were presented using the same apparatus as in Experiments 1 – 4. Each imperative stimulus was a naturalistic or a schematic representation of a human or a robotic hand in an opened or a closed posture. The four stimulus formats (human naturalistic, robotic naturalistic, human schematic, robotic schematic) are shown in Figure 11. Each imperative stimulus posture was preceded by a warning stimulus representing a neutral posture of the same hand type (human or robotic) in the same style



A Human naturalistic **B Robotic naturalistic**



C Human schematic **D Robotic schematic**

Figure 11: The stimuli used in Experiment 5, A Human naturalistic, B Robotic naturalistic, C Human schematic, D Robotic schematic. Within each stimulus type, the top image is the warning stimulus and the two images below are the opened (left) and closed (right) imperative stimuli.

Stimulus type	**Stimulus style**	**Posture**	**Width** Degrees of visual angle	**Height** Degrees of visual angle	**Relative luminance**	**Surface area** cm²
Human	Naturalistic	Opened	20.2	16.7	75	154
		Neutral	10.7	16.4	75	109
		Closed	10.6	13.6	68	94
Robotic	Naturalistic	Opened	20.2	16.4	93	67
		Neutral	10.4	18.5	96	67
		Closed	9.7	12.5	89	66
Human and robotic	Schematic	Opened	15.7	15.7	127	103
		Neutral	7.5	17.0	127	77
		Closed	7.5	12.0	127	68

Table 1: Experiment 5. Visual angle, luminance and surface area values for each posture of each stimulus type and style. Relative luminance was measured on a scale between 0 (completely black) and 255 (completely white).

(naturalistic or schematic).

Details of the size (width and height), luminance and surface area of the stimuli are given in Table 1. The schematic human and robotic stimuli differed in shape but were controlled for colour (all were blue), size, luminance and surface area. The naturalistic human and robotic stimuli differed in shape, colour palette (flesh vs. metallic tones), luminance and surface area. The human stimuli were slightly brighter, and occupied a larger area of the screen. Although not identical, the sizes of the naturalistic human and robotic stimuli were similar. The human hands appeared approximately life-size.

Data recording and analysis were performed using the same methods as in Experiments 1 – 4.

Procedure

The procedure was the same as that of Experiments 1 – 4 except as follows. In each block of the simple RT task, participants were now required to make a pre-specified response (to open or to close their right hand) as soon as an imperative stimulus *posture* (opened or closed) appeared on the screen. They were instructed to refrain from moving their hand in catch trials, when the imperative stimulus postures were not presented. Human naturalistic, robotic naturalistic, human schematic and robotic schematic stimuli were presented in separate blocks. Participants completed four blocks with each of these four stimulus formats, two in which closing was the required response and two in which opening was the required response. Testing was conducted over two days, with one open response and one close response block of each stimulus type completed each day.

The warning stimulus was presented for 800-1500ms before presentation of the imperative stimulus. SOA varied randomly between 800 and 1500ms in 50ms steps. In catch trials, the warning stimulus remained on the screen for 1980ms. Each block presented, in random order, 15 trials in which the imperative stimulus was an opened posture, 15 trials in which the imperative stimulus was a closed posture, and six catch trials. Before testing commenced in each block, participants completed five practice trials (two open stimulus, two close stimulus and one catch trial) with the response, and the stimuli, to be used in that block.

Within each day, blocks requiring the same response were completed consecutively, and those involving the same stimulus type (human or robotic) were also completed in immediate succession. For each participant, the order of stimulus formats (human naturalistic, robotic naturalistic, human schematic and robotic schematic) was the same for blocks in which they were making open and close responses, and constant across the first and second days of testing. The order in which responses were tested (open first or close first), and the order of blocks distinguished by stimulus type (human first or robotic first) and stimulus style (schematic first or naturalistic first) were counterbalanced.

4.1.2 Results and discussion

Participants initiated movement in 3.0% of catch trials. These data were not analysed further. Practice trials, incorrect responses (0.02%) and response omissions (0.04%) were excluded from the analysis, as were all RTs smaller than 100ms and greater than 1000ms (0.05%). The RT data, shown in Figure 12, were subjected to ANOVA in which stimulus-response compatibility (compatible and incompatible), stimulus type (human

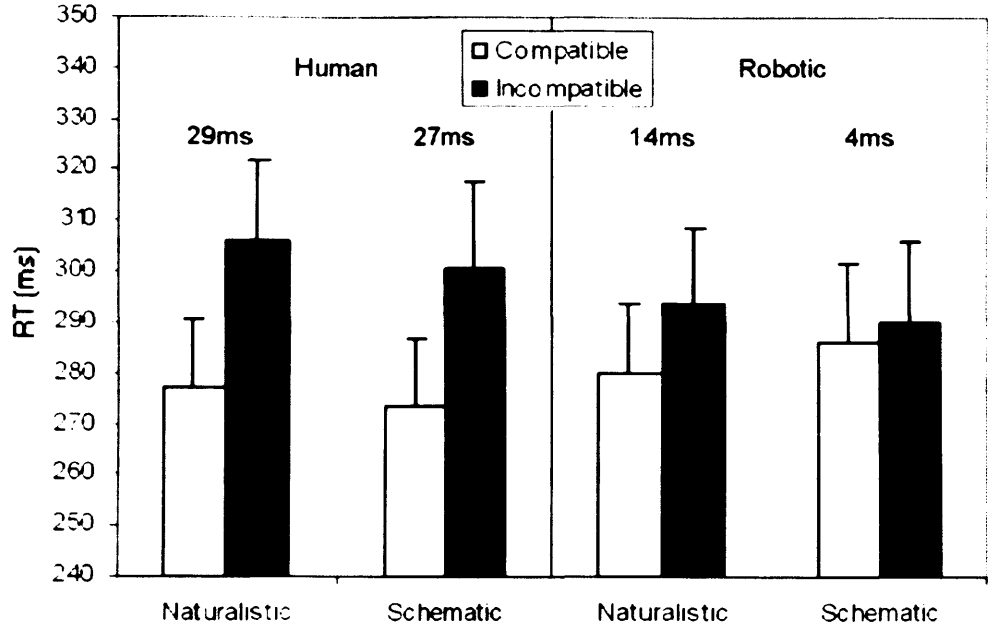


Figure 12: Experiment 5. Mean RT on compatible (open bars) and incompatible (shaded bars) trials for the human naturalistic, human schematic, robotic naturalistic and robotic schematic stimuli. Vertical bars indicate the standard error of the mean and numbers indicate the magnitude of the compatibility effect.

and robotic) and stimulus style (naturalistic or schematic) were within-subject variables. This analysis revealed a main effect of compatibility (F(1,15) = 21.4, p < 0.001), and a stimulus type x compatibility interaction (F(1,15) = 25.1, p < 0.001). On average, responding was 18ms faster on compatible trials (M = 279.2ms, SEM = 13.7ms) than on incompatible trials (M = 297.5ms, SEM = 15.9ms), and the compatibility effect was greater when participants were responding to human stimuli (27.9ms) than when they were responding to robotic stimuli (8.8ms). No other effects or interactions were significant.

The three-way compatibility x stimulus type x stimulus style interaction was not significant (F(1,15) = 3.0, p = 0.1). However, as indicated in Figure 12, it appeared that the compatibility x stimulus type interaction was greater for schematic than for naturalistic stimuli. Given that this experiment was investigating whether both stimulus sets were appropriate for use in Experiments 6 and 7, data from each stimulus style were analysed separately to check whether the human imitative bias was present with both naturalistic and schematic stimulus styles. Each of these analyses revealed a significant compatibility x stimulus type interaction, confirming that, both when the stimuli were naturalistic ($F(1,15) = 8.8$, $p = 0.01$), and when they were schematic ($F(1,15) = 29.8$, $p < 0.001$), the tendency to respond faster on compatible than on incompatible trials was greater when the stimulus hand was human than when it was robotic. Both naturalistic and schematic stimuli could therefore be used in Experiments 6 and 7.

The ASL model (and maybe the AIM model) might predict that there should have been a larger human imitative bias with naturalistic than schematic stimuli. Relative to human schematic stimuli, human naturalistic stimuli look more similar to those stimuli which are encountered often during life. Given that the ASL model assumes that any perceptible features of a stimulus can become associated with a response, not only spatial features which were represented in schematic stimuli, human naturalistic stimuli may therefore have been expected to elicit larger automatic imitation effects than human schematic stimuli. Therefore, the naturalistic stimuli may have been expected to evoke a larger human imitative bias. However, the observation that naturalistic stimuli do not elicit a larger human imitative bias than schematic stimuli is not problematic for the ASL model because Experiment 5 was not designed to investigate effects of stimulus style. For this reason, spatial features of naturalistic and schematic stimuli were not matched. In addition, luminance was not matched such that schematic stimuli may have been more salient. It is therefore not possible to draw many inferences from this comparison.

Therefore, the results of Experiment 5 confirm that human stimuli are more effective in eliciting automatic imitation than robotic stimuli, and that this human imitative bias can be detected using terminal postures as well as explicit movement stimuli.

4.2 Experiment 6

Experiment 6 investigated whether automatic imitation of robotic stimuli, and hence, the human imitative bias, could be modulated through training. Training paradigms have been used in several studies to modulate simple spatial compatibility effects, which suggest that spatial compatibility effects are mediated by stimulus-response associations established through experience. Tagliabue, Zorzi, Umilta, & Bassignani (2000) compared the effects of spatially compatible and incompatible training on performance in a spatial Simon task (Simon, Hinrichs, & Craft, 1970). Compatible training consisted of a choice RT task, where participants were required to press a right response key when an outline square stimulus was presented to the right of body midline, and a left response key when it was presented to the left. Incompatible training consisted of pressing a left response key when the outline square stimulus was presented to the right of body midline, and a right response key when it was presented to the left. Five minutes, 24 hours and one week later, participants were required to press the right and left keys in response to outline and solid square stimuli presented on the left or the right of the screen. Thus, in the test session, the type of square was the response-relevant dimension, and screen location was the response-irrelevant dimension. In this Simon task, responses in the compatible training group were faster when the square requiring a right response appeared on the right, rather than the left, side of the screen, and when the square requiring a left response appeared on the left, rather than the right, side of the screen. In contrast, the group who had received incompatible training showed no such spatial compatibility effects on test. This finding that spatially compatible and incompatible training can modulate spatial compatibility effects has been replicated by others (Vu, Proctor, & Urcuioli, 2003; Tagliabue, Zorzi, & Umilta, 2002).

As discussed in Chapter 1, one experiment has used a training paradigm to assess the effects of experience on automatic imitation. During training, Heyes et al. (2005) required a compatible training group to open their hand whenever a human stimulus hand opened, and to close their hand whenever it closed. In contrast, participants in an incompatible training group were required to open their hand whenever a human stimulus hand closed, and close their hand whenever it opened. The group given compatible training subsequently showed an automatic imitation effect; when required to perform a pre-specified response (e.g. open their hand) upon movement of a stimulus hand, they were faster to execute this response when it was compatible (opening) with the stimulus movement rather than incompatible (closing). The incompatible training group did not show an automatic imitation effect.

Experiment 6 employed a training paradigm similar to that used by Heyes et al. (2005), but training involved only robotic stimuli, and the effects of training on automatic imitation of robotic stimuli were compared with the effects of training on imitation of human stimuli which were not presented during training. Participants first completed a pre-test session with both human and robotic stimuli to assess automatic imitation with these two stimulus types. Twenty-four hours later, they completed a training session with only robotic stimuli, and 24 hours after this they completed a post-test session with both human and robotic stimuli to further assess automatic imitation of these two stimulus types. During training, the compatible training group (group CT) were instructed to open their hand whenever they detected an opened stimulus hand and close their hand whenever they detected a closed stimulus hand. The incompatible training group (group IT) were instructed to open their hand whenever they detected a closed stimulus hand and close their hand whenever they detected an opened stimulus hand.

The AIM model would predict that automatic imitation of robotic stimuli and the human imitative bias should not be modulated by training with robotic stimuli, therefore automatic imitation of robotic stimuli should not change systematically between groups CT and IT from pre- to post-test. In contrast, the ASL model would predict that automatic imitation of robotic stimuli should increase from pre- to post-test in group CT, relative to group IT. The human imitative bias should therefore decrease from pre- to post in group CT, relative to group IT.

4.2.1 Method

Participants

Twenty new, consenting, healthy volunteers with an average age of 24.4 years, eight male, participated in Experiment 6, and were paid a small honorarium for their participation. Four participants were excluded from training and post-test sessions because they did not demonstrate numerically larger automatic imitation effects with human stimuli than robotic stimuli at pre-test. This experiment investigated modulation of the human imitative bias, and therefore it was important that all participants undergoing training displayed this initial bias. The remaining 16 participants were randomly assigned in equal numbers to groups CT and IT.

The stimuli were identical to those used in Experiment 5. Data recording and analysis were performed using the same methods as in Experiment 5.

Procedure

Each participant completed three sessions, with 24 hours separating each session. In the first session, the pre-test session, and the third session, the post-test session, they completed the procedure described in Experiment 5. In the second session, the training session, participants received one of two types of training with the robotic stimuli. In a choice RT task, group CT were instructed to respond to an opened stimulus by opening their hand, and to a closed stimulus by closing their hand. Group IT were instructed to respond to an opened stimulus by closing their hand and to a closed stimulus by opening their hand. Robotic naturalistic and robotic schematic stimuli were presented in separate blocks. Participants completed six blocks with each of these two stimulus formats. Blocks involving naturalistic and schematic stimuli were alternated. Training lasted approximately 45 minutes in total, including a short rest between blocks.

During training, as during test, all trials began with presentation of the warning stimulus. This was replaced 1000ms later by an imperative stimulus (opened or closed robotic hand) which was of 480ms duration. After presentation of the imperative stimulus, the screen went black for 3000ms before the warning stimulus for the next trial appeared.

Each block presented, in random order, 18 trials in which the imperative stimulus was an opened posture and 18 trials in which the imperative stimulus was a closed posture.

Before testing commenced in the first training block with each stimulus style (naturalistic or schematic), participants completed six practice trials (three open stimulus, three close stimulus) with the stimuli and responses to be used in that block. The order of blocks distinguished by stimulus style (schematic first or naturalistic first) was counter-balanced.

4.2.2 Results

Training

Practice trials, incorrect responses (1.59%) and response omissions (0.09%) were excluded from the analysis, as were all RTs smaller than 100ms and greater than 1000ms (0.09%). Figure 13 shows, for each of the two groups, mean RT in each training block. These data were subjected to ANOVA in which block (1-6) was a within-subject variable and training type (CT and IT) was a between-subject variable. The analysis revealed significant main effects of block ($F(5,70) = 6.9$, $p < 0.001$, Greenhouse Geisser corrected) and training type ($F(1,14) = 12.6$, $p < 0.005$). The block x training type interaction was not significant ($F < 1$). A supplementary linear trend analysis confirmed that the effect of block was created by a downward trend in RT over block ($F(1,14) = 14.6$, $p = 0.002$). Thus, as can be seen in Figure 13, responding was faster in later blocks, when participants had greater experience with the stimuli and task than in earlier blocks, providing evidence that training was effective. Also, as expected on the basis of automatic imitation, responding was slower in group IT than in group CT.

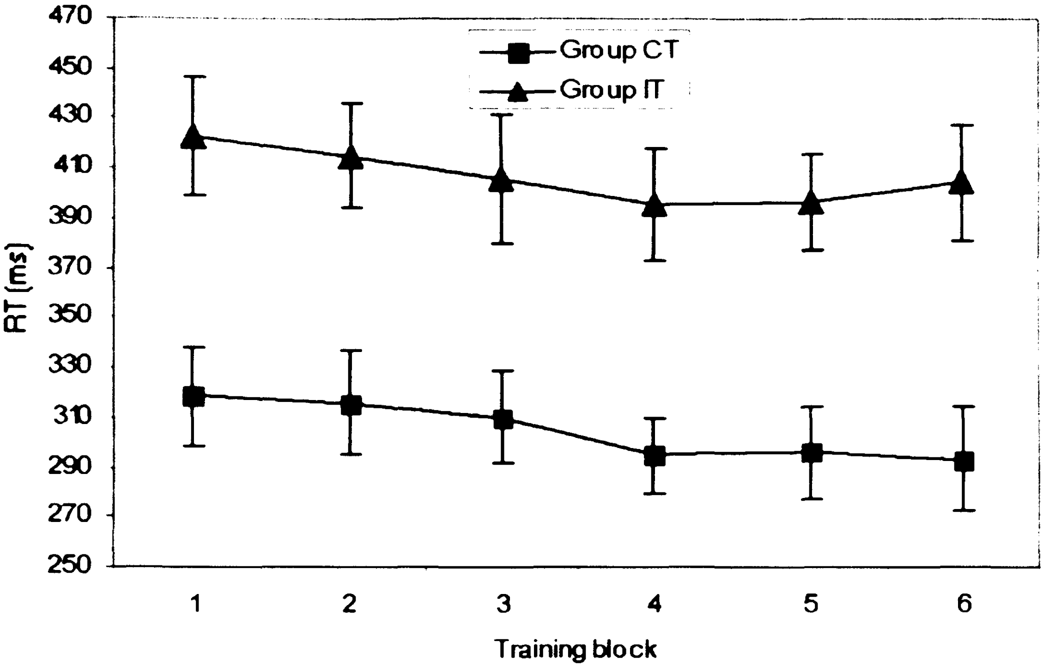


Figure 13: Experiment 6. Mean RT for each training block. Squares represent RTs for those receiving compatible training (group CT) and triangles represent RTs for those receiving incompatible training (group IT). Vertical bars indicate the standard error of the mean.

Pre- and post-test

During the test sessions, participants initiated movement in 3.8% of catch trials. These data were not analysed further. Practice trials, incorrect responses (0.09%) and response omissions (0.14%) were excluded from the analysis, as were all RTs smaller than 100ms and greater than 1000ms (0.01%).

Pre-test

All 20 participants were included in the preliminary analysis of pre-test data, including the four who did not demonstrate a human imitative bias and therefore did not subsequently participate in training and post-test sessions. This analysis was performed to confirm whether Experiment 6 replicated Experiment 5 and found a human imitative bias with these stimuli before any training. These data were subjected to ANOVA in which stimulus-response compatibility (compatible and incompatible), stimulus type (human and robotic) and stimulus style (naturalistic or schematic) were within-subject variables. This analysis revealed a main effect of compatibility ($F(1,19) = 58.5$, $p < 0.001$), and a stimulus type x compatibility interaction ($F(1,19) = 11.5$, $p < 0.005$). On average, responding was 26ms faster on compatible trials (M = 275.4ms, SEM = 10.8ms) than on incompatible trials (M = 300.9ms, SEM = 11.7ms), and the compatibility effect was greater when participants were responding to human stimuli (32ms) than when they were responding to robotic stimuli (19ms). No other effects or interactions were significant. These findings therefore replicate those in Experiment 5 of a human imitative bias present before any training.

Pre- vs. post-test

The RT data can be seen in Figure 14, where the height of the bars indicates mean RT, and Figure 15, where the height of the bars indicates the magnitude of the compatibility effect, calculated by subtracting RT on compatible trials from RT on incompatible trials. Only the 16 participants who participated in all three sessions were included in this analysis. Examination of Figures 14 and 15 suggests that, in group CT automatic imitation of robotic stimuli increased from pre- to post- test, relative to group IT, indicating an influence of training type on automatic imitation. In comparison, automatic imitation of human stimuli decreased from pre- to post-test in group CT and group IT. This decrease may be smaller in group CT compared to group IT, but the influence of training type on automatic imitation of human stimuli appears smaller than the influence of training type on automatic imitation of robotic stimuli. Therefore, the greater

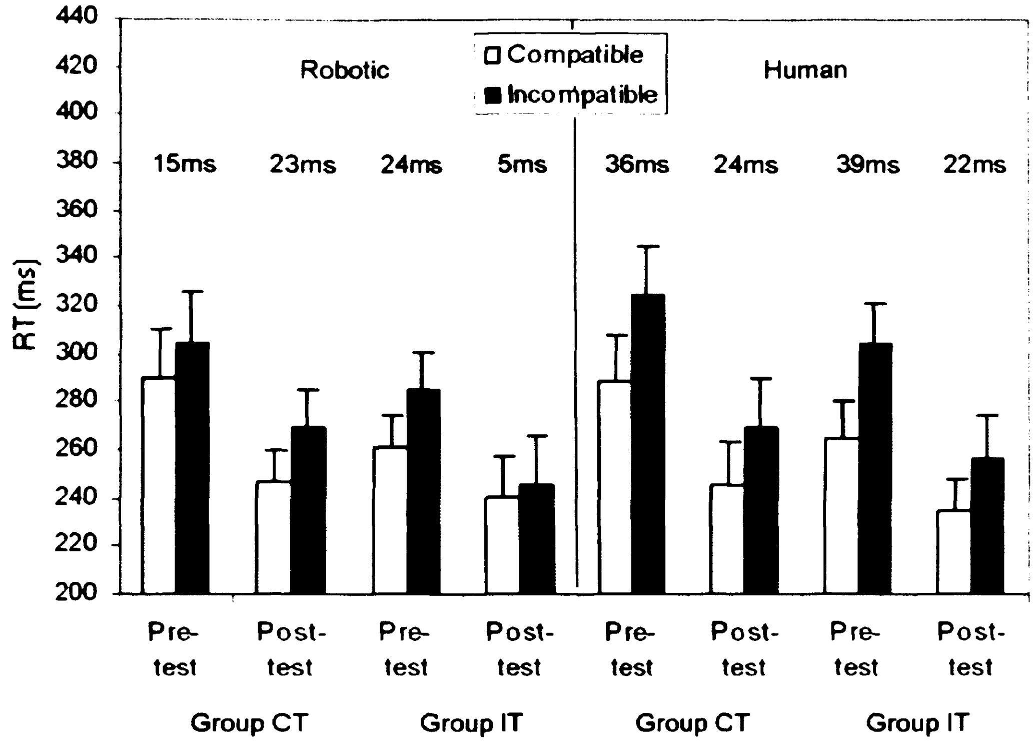


Figure 14: Experiment 6. Mean RT on compatible (open bars) and incompatible (shaded bars) trials, pre- and post-test in group CT and group IT for robotic and human stimuli. Vertical bars indicate the standard error of the mean and numbers indicate the magnitude of the compatibility effect.

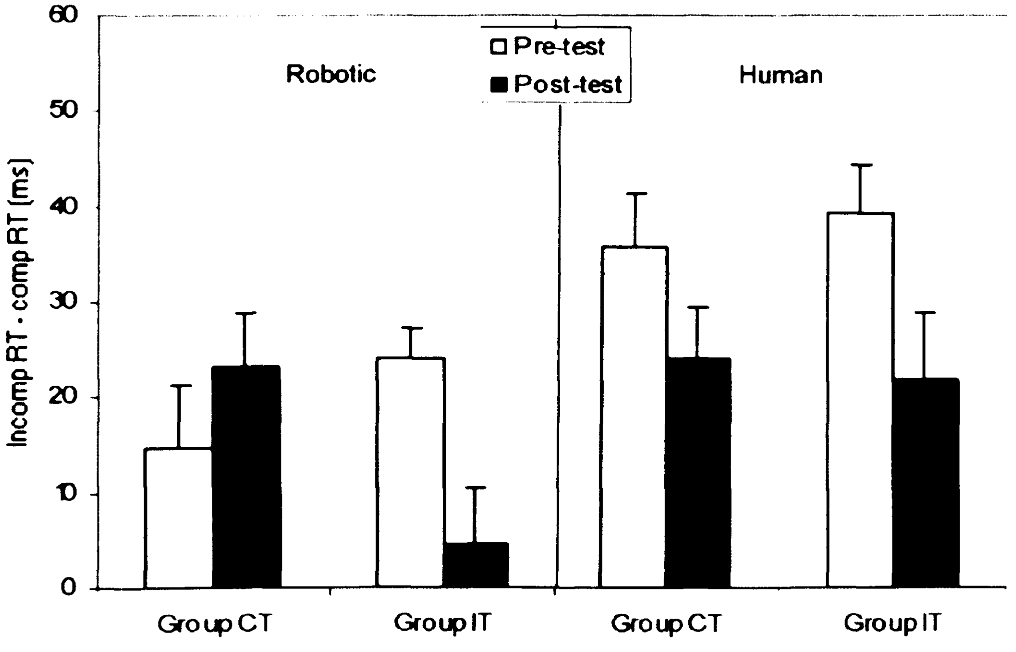


Figure 15: Experiment 6. Mean RT on incompatible trials minus mean RT on compatible trials pre- (open bars) and post-test (shaded bars) in group CT and group IT for robotic and human stimuli. Vertical bars indicate the standard error of the mean.

influence of training type on automatic imitation of robotic stimuli resulted in a reduction in the human imitative bias from pre- to post- test in group CT, relative to group IT.

These observations were supported by ANOVA in which stimulus-response compatibility (compatible and incompatible), stimulus type (human and robotic) and test session (pre-test and post-test) were within-subject variables. Training type (CT or IT) was a between-subject variable. There was a four-way session x compatibility x stimulus type x training type interaction ($F(1,14) = 15.7$, $p = 0.001$). Separate analyses of RTs to robotic and human stimuli indicated a session x compatibility x training type interaction with robotic stimuli ($F(1,14) = 10.1$, $p < 0.01$) but not with human stimuli ($F < 1$). There was a compatibility x stimulus type x training type interaction at post-test ($F(1,14) = 9.4$, $p < 0.01$) but there was no evidence of such an interaction at pre-test ($F(1,14) = 1.4$, $p = 0.3$).

4.2.3 Discussion

The results of Experiment 6 provide evidence that automatic imitation effects with robotic stimuli are larger following compatible training with those stimuli, relative to incompatible training. This resulted in a reduction in the human imitative bias following compatible training, relative to incompatible training. This pattern of results is consistent with the ASL model of imitation which predicts that the human imitative bias results from greater opportunities for associative learning between human stimuli and matching responses. This pattern of results is inconsistent with the AIM model of imitation which predicts that training should have no systematic influence on automatic imitation potentials and hence, the human imitative bias, because imitation mechanisms are innate.

4.3 Experiment 7

Experiment 6 found evidence that automatic imitation of robotic stimuli is greater following compatible training with those stimuli, relative to incompatible training. However, caution is necessary in interpreting the effects of training. A distinction has been drawn in the literature on cognitive control between long-term associations, established on the basis of practice and postulated by the ASL model to mediate imitation, and short-term associations, established on the basis of task instructions (e.g. Tagliabue et al., 2000; Barber & O'Leary, 1997; De Jong, 1995; McClelland, McNaughton, & O'Reilly, 1995; Shaffer, 1965). When given task instructions, short-term associations are thought to operate via executive functions which map task-appropriate responses to stimuli. These associations are therefore thought to rely on a fronto-parietal network including left fronto-lateral cortex, pre-supplementary motor area and bilateral intraparietal sulcus (e.g. Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Pollmann, Dove, von Cramon, & Wiggins, 2000). In contrast, long-term associations are not established on the basis of instructions, but on the basis of practice, when the conditions are presented for associative learning. In addition, long-term associations do not operate via executive functions but are direct associations between stimulus and response representations (see also Redding & Wallace, 2006a; Redding & Wallace, 2006b; Redding, Rossetti, & Wallace, 2005).

Evidence of the formation of short-term associations was provided by De Houwer, Beckers, Vandorpe, & Custers (2005). Participants were informed that they should respond to the words 'left' and 'right' with vocal responses 'bee' and 'boo' respectively, and also to blue and green squares with vocal responses 'bee' and 'boo' respectively.

Despite the fact that left and right stimuli were never actually presented, participants were faster to respond 'bee' to blue squares presented on the left, rather than the right, of the screen, and 'boo' to green squares presented on the right, rather than the left, of the screen. These effects cannot result from formation of long-term associations because participants did not actually perform 'bee' responses to left stimuli and 'boo' responses to right stimuli. However, the task set established on the basis of instructions appears to have created a spatial compatibility effect.

In contrast to the findings of De Houwer et al. (2005), findings of Kunde (2004) are likely to depend on modulation of long-term associations. In a training phase, Kunde (2004) required participants to press left and right response keys. Left key presses resulted in presentation of upward-pointing arrows, and right key presses resulted in presentation of downward-pointing arrows. In a subsequent test phase, participants were faster to execute key presses (e.g. left) in response to stimuli which had followed them in training phases (upward-pointing arrows), than in response to stimuli which had not followed them (downward-pointing arrows). Elsner & Hommel (2001; 2004) have reported similar effects of 'response-outcome' learning when associating left and right key presses with high and low tones during training. These effects are unlikely to reflect formation of short-term associations, because there is no reference to the stimulus-response relationship in the instructions given prior to training. These effects are therefore more likely to reflect formation of long-term associations, established on the basis of task practice.

Although the results of Experiment 6 are consistent with influences of training on long-term associations, they are also consistent with influences of training on short-term associations, because task set switching is associated with an RT cost (e.g. Allport, Styles, & Hsieh, 1994; Biederman, 1972; Jersild, 1927). Participants in group CT would have established a task set during training to perform movements which were compatible with those of a robotic hand. When these participants were required to perform responses which were incompatible with movements of robotic stimuli at post-test, the task was different to training and RTs may therefore have been slowed. This task-switching RT cost may have resulted in larger compatibility effects at post-test, relative to pre-test. In contrast, participants in group IT would have established a task set during training to perform movements which were incompatible with those of a robotic hand. When these participants were required to perform responses which were compatible with movements of robotic stimuli at post-test, RTs may therefore have been slowed, hence resulting in smaller compatibility effects at post-test, relative to pre-test.

It is important to investigate whether the effects of training observed in Experiment 6 reflect formation of short-term associations established on the basis of task instructions or long-term associations developed through practice. If the effects of training reflect task instructions and not practice, this result would not provide support for the ASL model of imitation and the human imitative bias, and would also be consistent with the AIM model of imitation. Although the AIM model is inconsistent with modulation of long-term associations between stimuli and responses, it does not appear inconsistent with influences of task set on response speed.

Experiment 7 therefore employed a training paradigm similar to that used in Experiment 6 but there was no reference to the stimulus-response relationship in the instructions given prior to training. In Experiment 7, pre- and post-test sessions were identical to those in Experiment 6. However, during training sessions, a '1' or '2' presented on the warning stimulus instructed participants which response they should prepare to execute. Participants were instructed to prepare to open their hand when a 1 was presented, and to prepare to close their hand when a 2 was presented, but to refrain from executing the response until the imperative stimulus posture was presented. In group CT, this imperative stimulus posture was compatible with the required response, and in group IT, this posture was incompatible with the required response. For example, when a '1' was presented (requiring an opening response), this was followed in group CT by an opened robotic hand and in group IT by a closed robotic hand.

If the effects of training observed in Experiment 6 are at least partially due to formation of long-term associations established on the basis of practice during training, automatic imitation effects with robotic stimuli should increase from pre- to post-test in group CT, relative to group IT. This finding would be consistent with the ASL model of imitation and inconsistent with the AIM model. However, if the effects of training observed in Experiment 6 reflect only formation of short-term associations established on the basis of task instructions given prior to training, Experiment 7 should find no influence of training on automatic imitation of robotic stimuli. This outcome would be consistent with the AIM model of imitation and not with the ASL model.

4.3.1 Method

Participants

Twenty-eight new, consenting, healthy volunteers with an average age of 22.0 years, nine male, participated in Experiment 7, and were paid a small honorarium for their participation. Four participants were excluded from training and post-test because they did not demonstrate larger imitation effects with human stimuli than robotic stimuli at pre-test. The remaining 24 participants were randomly assigned in equal numbers to groups CT and IT.

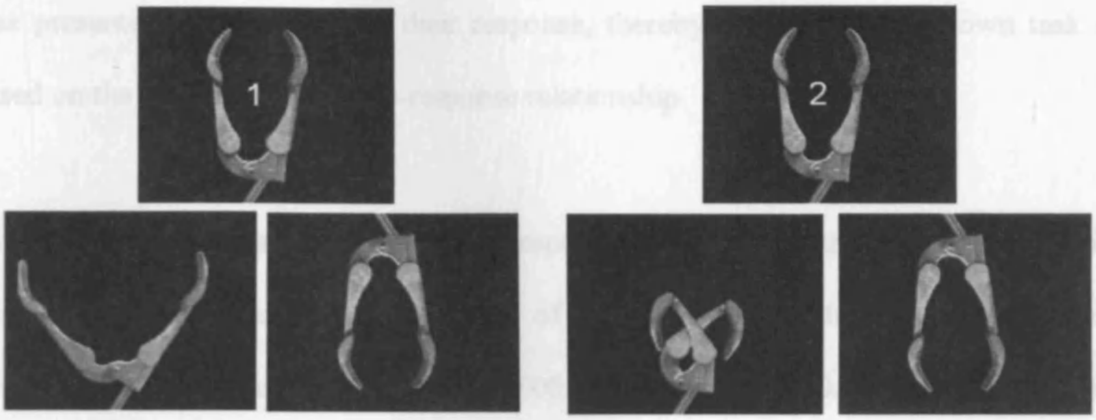
Stimuli

The stimuli used in pre- and post-test sessions were identical to those used in Experiments 5 and 6. The stimuli used in training sessions were the same as those used in Experiments 5 and 6 except as follows. On the warning stimulus, a 1 or 2 was inserted between the two 'fingers' of the hand (see Figure 16). On catch trials, the imperative stimulus was an inverted neutral hand.

Data recording and analysis were performed using the same methods as in Experiments 5 and 6.

Procedure

The procedure was the same as that of Experiment 6 except as follows. The training



Open Catch
A Open response trials in group CT

Close Catch
B Close response trials in group CT

Figure 16: The stimuli used in training sessions in Experiment 7, A Open response trials in group CT, B Close response trials in group CT. Within each stimulus type, the image at the top is the warning stimulus, the image on the left is the imperative stimulus posture presented on 90% of trials and the image on the right is the catch imperative stimulus posture presented on 10% of trials.

session consisted of a choice RT task in which both training groups were required to prepare to execute an opening response whenever a ‘1’ was presented on the warning stimulus, and to prepare to execute a closing response whenever a ‘2’ was presented on the warning stimulus. Participants were required to execute this prepared response when the imperative stimulus posture was presented. In group CT, on 90% of trials the imperative stimulus represented the movement type which was the same as that which participants were required to perform. Thus, a 1 was followed by an open posture, and a 2 was followed by a closed posture. In group IT, on 90% of trials the imperative stimulus represented the movement type which was opposite to that which participants were required to perform. The other 10% of trials were catch trials, in which the imperative stimulus was an inverted neutral hand, and participants were still required to select their response on the basis of the number presented on the warning stimulus. The occurrence of these catch trials ensured that participants could not wait until the imperative stimulus was presented before selecting their response, thereby establishing their own task set based on the imperative stimulus-response relationship.

Given that participants now knew which response to perform on the basis of the warning stimulus, the SOA between presentation of the warning stimulus and the imperative stimulus now varied randomly between 800 and 1500ms, in 50ms steps. Each block presented, in random order, 18 trials in which the imperative stimulus was an opened posture, 18 trials in which the imperative stimulus was a closed posture, and four catch trials in which the imperative stimulus was an inverted neutral posture.

4.3.2 Results

Training

Participants performed correct responses on all catch trials. Practice trials, incorrect responses (1.10%) and response omissions (0.57%) were excluded from the analysis, as were all RTs smaller than 100ms and greater than 1000ms (2.03%). Figure 17 shows, for groups CT and IT, mean RT in each training block. These data were subjected to ANOVA in which block (1-6) was a within-subject variable and training type (CT and IT) was a between-subject variable. The analysis revealed no significant main effects or interactions. The main effect of block was not reliable ($F(5,110) = 1.6$, $p = 0.2$, Greenhouse Geisser corrected) and neither was the main effect of training type ($F(1,22) = 2.7$, $p = 0.1$). As a further test for any effects of decrease in RT over block, a supplementary linear trend analysis was performed on the data. Similar to the standard ANOVA, this analysis did not find a reliable effect of block ($F(1,22) = 3.3$, $p = 0.08$).

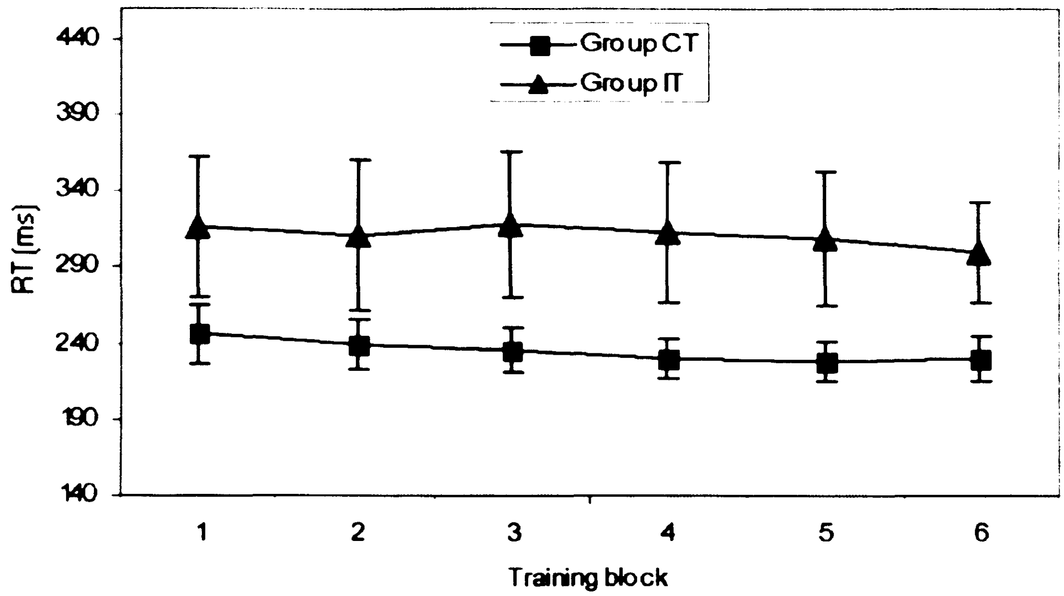


Figure 17: Experiment 7. Mean RT for each training block. Squares represent RTs for those receiving compatible training (group CT) and triangles represent RTs for those receiving incompatible training (group IT). Vertical bars indicate the standard error of the mean.

It may seem surprising that the effect of training type was not reliable, given that an effect would have indicated automatic imitation, and that this effect was observed in Experiment 6. However, as can be seen in Figure 17, mean RT in Experiment 7 during training was much shorter (M = 273.1ms, SEM = 23.3ms) than mean RT in Experiment 6 (M = 355.7ms, SEM = 12.4ms) (F(1,36) = 7.1, $p < 0.02$). This difference suggests that, as instructed, participants were selecting their response on the basis of the number presented on the warning stimulus in Experiment 7, leading to more complete preparation of the response when the imperative stimulus posture was presented relative to Experiment 6. This change in task appears to have resulted in a smaller effect of training type. When this smaller effect of training type is coupled with the fact that the comparison was made between-subject (cf. most other automatic imitation effects reported in this thesis), it is less surprising that the effect was not reliable.

To confirm that participants were selecting their response on the basis of the 1 or 2 presented on the warning stimulus, rather than on the basis of the imperative stimulus posture, the RT training data were analysed with reference to SOA. If participants were selecting their response on the basis of the 1 or 2 presented on the warning stimulus, then they should have been faster to execute this response when there was longer to prepare it, that is, following a longer SOA (Niemi & Näätänen, 1981). However, if participants were selecting their response on the basis of the imperative stimulus posture, there should have been no such influence of SOA on RT. The data were divided into three bins of SOA (800-1000ms, 1050-1250ms, and 1300-1500ms), and subjected to ANOVA in which block (1-6) and SOA (800-1000ms, 1050-1250ms, and 1300-1500ms) were within-subject variables and training type (CT and IT) was a between-subject variable. The analysis indicated that participants were selecting their response on the basis of the number; responses following an SOA of 1300-1500ms were fastest ($\underline{M}$ = 262.5ms, $\underline{SEM}$ = 24.1ms), followed by responses following an SOA of 1050-1250ms ($\underline{M}$ = 269.9ms, $\underline{SEM}$ = 24.1ms), and responses following an SOA of 800-1000ms were slowest ($\underline{M}$ = 287.7ms, $\underline{SEM}$ = 23.6ms) ($F(2,44) = 31.2$, $p < 0.001$, Greenhouse Geisser corrected). Further confirmation that participants were selecting their response on the basis of the number is provided by the observation that participants performed correct responses on all catch trials, where the posture stimulus did not provide information concerning which response was correct.

Pre- and post-test

On test, participants initiated movement in 2.1% of catch trials. These data were not analysed further. Practice trials, incorrect responses (0.51%) and response omissions

(0.21%) were excluded from the analysis, as were all RTs smaller than 100ms and greater than 1000ms (0.08%).

Pre-test

All 28 participants were included in the analysis of pre-test data, including those four who did not demonstrate a human imitative bias and did not subsequently participate in training and post-test sessions. These data were subjected to ANOVA in which stimulus-response compatibility (compatible and incompatible), stimulus type (human and robotic) and stimulus style (naturalistic or schematic) were within-subject variables. This analysis revealed a main effect of compatibility ($F(1,27) = 60.6$, $p < 0.001$), and a stimulus type x compatibility interaction ($F(1,27) = 14.7$, $p = 0.001$). On average, responding was 29ms faster on compatible trials (M = 299.7ms, SEM = 15.1ms) than on incompatible trials (M = 329.1ms, SEM = 16.9ms), and the compatibility effect was greater when participants were responding to human stimuli (41ms) than when they were responding to robotic stimuli (18ms). These findings replicate those of Experiments 5 and 6, indicating that the current procedure reliably detects a human imitative bias present before any training. No other effects or interactions were significant.

Pre- vs. post-test

The RT data are shown in Figure 18, where the height of the bars indicates mean RT, and in Figure 19, where the height of the bars indicates the size of the compatibility effect (RT on incompatible trials minus RT on compatible trials). Only the 24 participants who participated in all three sessions were included in this analysis. Analysis of Figures 18

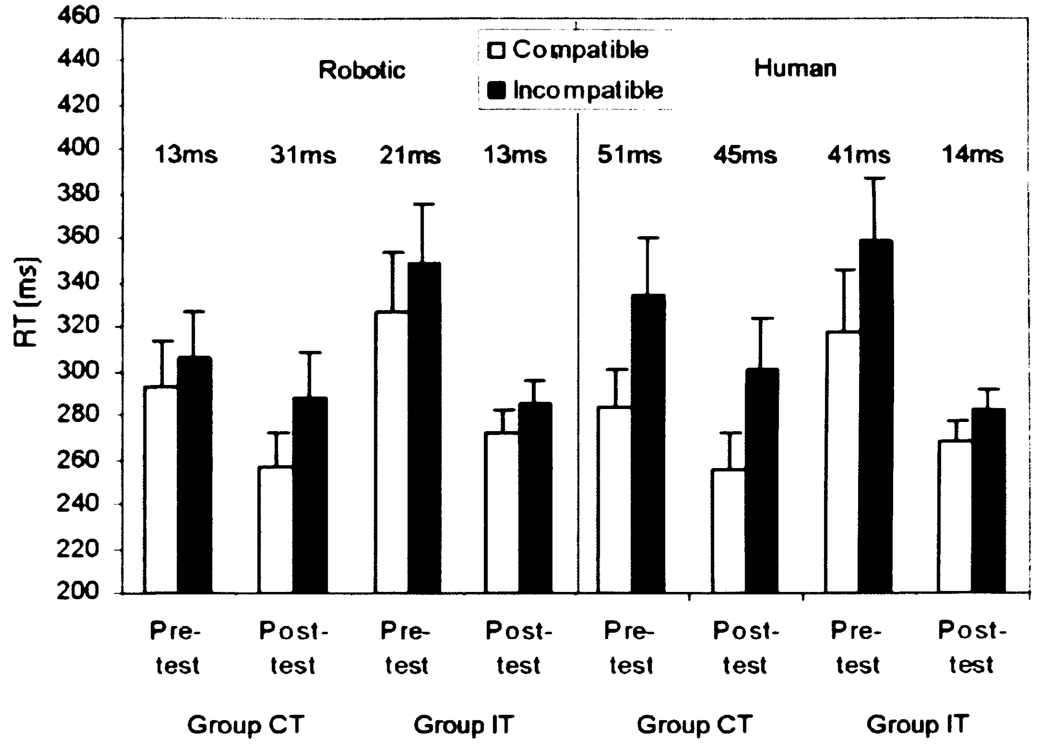


Figure 18: Experiment 7. Mean RT on compatible (open bars) and incompatible (shaded bars) trials for robotic and human stimuli, pre- and post-test, in group CT and group IT. Vertical bars indicate the standard error of the mean and numbers indicate the magnitude of the compatibility effect.

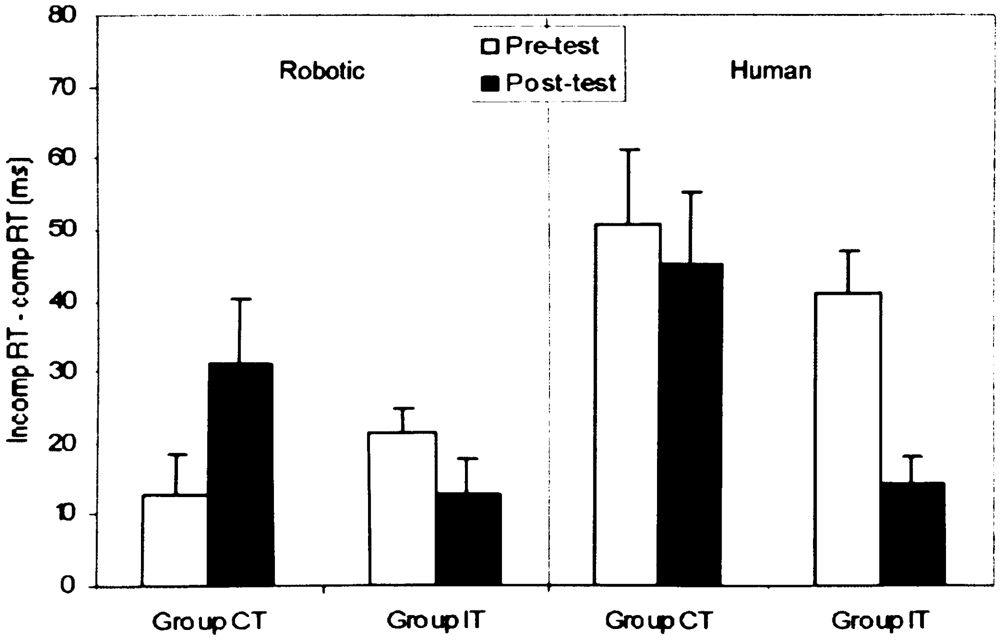


Figure 19: Experiment 7. Mean RT on incompatible trials minus mean RT on compatible trials for human (open bars) and robotic (shaded bars) stimuli, pre- and post-test, in group CT and group IT. Vertical bars indicate the standard error of the mean.

and 19 suggests that, as in Experiment 6, automatic imitation of robotic stimuli increased from pre- to post-test in group CT, relative to group IT, indicating an influence of training type on automatic imitation. In comparison, automatic imitation of human stimuli decreased from pre- to post-test in group CT and group IT, but this decrease appears greater in group IT than in group CT. The influence of training type on automatic imitation of human stimuli appears as strong as the influence of training type on automatic imitation effects with robotic stimuli.

These observations were supported by ANOVA in which stimulus-response compatibility (compatible and incompatible), stimulus type (human and robotic) and session of testing (pre-test and post-test) were within-subject variables. Training type (CT or IT) was a between-subject variable. There was no evidence of a four-way session x compatibility x training type x stimulus type interaction ($F < 1$), or a compatibility x training type x stimulus type interaction either at pre-test ($F < 1$) or at post-test ($F(1,22) = 2.0$, $p = 0.2$). However, there was a three-way session x compatibility x training type interaction ($F(1,22) = 7.6$, $p < 0.02$). Separate analyses with robotic and human stimuli indicated a session x compatibility x training type interaction with both robotic ($F(1,22) = 4.7$, $p < 0.05$) and human stimuli ($F(1,22) = 4.5$, $p < 0.05$).

4.3.3 Discussion

Experiment 7 investigated whether the effects of training observed in Experiment 6 reflected formation of short-term associations established on the basis of task instructions, or long-term associations established on the basis of practice. Experiment 7 therefore employed a training paradigm which was similar to that used in Experiment 6, but instructions given prior to training did not refer to the stimulus-response relationship. If the effects of training observed in Experiment 6 reflected only formation of short-term associations, Experiment 7 should not have observed an influence of training. In contrast, if the effects of training observed in Experiment 6 at least partially reflected formation of long-term associations, Experiment 7 should have observed a similar influence of training. Like those of Experiment 6, the results of Experiment 7 indicated that automatic imitation of robotic stimuli increased following compatible training with those stimuli, relative to incompatible training. However, training also had an influence on automatic imitation of human stimuli; automatic imitation of human stimuli decreased from pre- to post-test to a greater extent in group IT than in group CT.

Notably, the effect of training type on compatibility with the human stimuli was different to the effect with the robotic stimuli, despite the similarity of the statistical interaction. Automatic imitation of robotic stimuli increased from pre- to post-test in group CT and decreased from pre- to post-test in group IT. In contrast, automatic imitation of human stimuli decreased from pre- to post-test in both training groups, but decreased by more in group IT. Two factors will now be outlined which may have contributed to the specific effects observable with each stimulus type. First, the decrease in automatic imitation from pre- to post-test which was observed with human stimuli in both training groups is likely to be driven by the faster responses at post-test, when participants have more experience with the stimuli and task. This interpretation would be consistent with the finding in previous studies that automatic imitation effects are larger with slower responses (e.g. Experiment 4 of this thesis, Bird, 2003; Brass et al., 2001). Second, the fact that this decrease was less dramatic with robotic stimuli may be driven by perceptual learning with robotic stimuli during training sessions. With exposure to robotic stimuli between pre- and post-test sessions, participants can learn to better discriminate opened and closed stimuli (e.g. Chamizo & Mackintosh, 1989; Gibson, 1969). This perceptual learning may lead to larger automatic imitation effects because features which distinguish the two movement types may be processed to a greater extent. Therefore, despite the apparent differences in effects of training on automatic imitation of human and robotic stimuli, there is no reason to assume that the influences of associative learning differ.

The influences of training on automatic imitation of human stimuli are therefore likely to result from generalisation of the training with robotic stimuli. Finding that experience will generalise to other stimuli is consistent with the ASL model of imitation; stimulus generalisation is a ubiquitous feature of associative learning (Pearce, 1987). The especially high levels of stimulus generalisation observed in Experiment 7 may be driven by two factors. First, 'acquired equivalence' (Hall, 1991) refers to the finding that one can learn an association between two events, through their common association with a third event (see Chapter 1). According to the ASL model, compatible responses are associated with human stimuli before training. During compatible training, robotic stimuli will become associated with these same responses. This common association with compatible responses may mean that human and robotic stimuli become associated. Therefore, when a robotic opened stimulus is presented during training, the visual representation of a human opened stimulus may also be activated. When the participant subsequently opens their hand, the association between an opened human stimulus and an opening response can strengthen, in addition to the association between an opened robotic stimulus and an opening response.

However, acquired equivalence may be expected to influence behaviour equally in Experiments 6 and 7. A second factor which may explain especially high generalisation in Experiment 7 is that the stimulus posture during training acted as an imperative stimulus and not a discriminative stimulus. Participants were only required to detect movement of some description on the screen, and may have paid less attention to the posture stimuli than in Experiment 6. This lack of attention could plausibly have resulted in participants processing only global features of the stimulus, such as approximate form (e.g. whether the fingers moved inwards or outwards), and these features are similar in human and robotic stimuli. Given that these features are similar in human and robotic stimuli, the stimulus may have been perceived as human in some trials and robotic in other trials, given that ambiguous stimuli tend to be perceived as one thing or another rather than ambiguous (e.g. Necker cube, Necker, 1832). Therefore, this provides a further explanation why training may have modified associations between human stimuli and responses as well as associations between robotic stimuli and responses.

The hypothesis that participants were processing only simple features of the stimuli in Experiment 7, compared with participants in Experiment 6, is consistent with the RT training data. In Experiment 6, RTs during training were fairly slow, and decreased in the course of the training session. This pattern suggests that stimuli were processed thoroughly before a response was selected, and, as the training session progressed, that participants became faster to identify stimulus features which discriminated opened and closed stimuli. In contrast, RTs during training in Experiment 7 were fast, and did not decrease during the training session, which suggests that participants could perform the task easily at the outset, processing only very obvious parts of the stimuli such as global form.

4.4 General discussion

The experiments reported in this chapter investigated whether automatic imitation of non-human stimuli (robotic) increased following compatible training with those stimuli, relative to incompatible training, and therefore whether the human imitative bias could be modulated through training. Experiment 5 established a human imitative bias with stimuli which could be used in training paradigms in Experiments 6 and 7. Experiment 6 indicated that automatic imitation of robotic stimuli increased from pre- to post-test in a compatible training group, relative to an incompatible training group. Therefore, the human imitative bias decreased from pre- to post-test in the compatible training group, relative to the incompatible training group. Due to the possibility that influences of training observed in Experiment 6 reflected formation of short-term associations established during training on the basis of task instructions, Experiment 7 investigated influences of training where instructions given prior to training did not refer to the stimulus-response relationship. Experiment 7 indicated, similarly to Experiment 6, that automatic imitation of robotic stimuli increased from pre- to post-test in the compatible training group, relative to the incompatible training group. These results are difficult to interpret in terms of formation of short-term associations, and are more likely to reflect formation of long-term associations, established on the basis of practice. However, unlike Experiment 6, Experiment 7 also observed an influence of training on automatic imitation of human stimuli. This resulted in no observation of modulation of the human imitative bias through training.

The finding in Experiments 6 and 7 that automatic imitation of robotic stimuli can be modulated through training, and that these effects are likely to reflect modulations of long-term associations, are consistent with the ASL model of imitation which claims that imitative capabilities arise through associative learning connecting the visual representations of action with matching responses. The findings in Experiments 6 and 7 are inconsistent with the AIM model of imitation. The AIM model posits that imitation is mediated by innate mechanisms, so training is unlikely to have a systematic effect on imitation of either human or non-human stimuli. In the face of any evidence of training effects, nativist accounts may try to defend themselves with reference to task sets, but it is difficult to interpret the findings of Experiment 7 in such a way.

The ASL model predicts that a human imitative bias arises through greater opportunities for associative learning with human stimuli than non-human stimuli. Therefore presenting compatible training with non-human stimuli should increase automatic imitation of those stimuli from pre- to post-test, relative to incompatible training, and the human imitative bias should decrease in a compatible training group from pre- to post-test, relative to an incompatible training group. However, the generalisation of training to human stimuli resulted in Experiment 7 detecting no influence of training on the human imitative bias. It might therefore be suggested that Experiment 7 provides no support for the ASL hypothesis of the human imitative bias, despite providing support for the ASL hypothesis of imitation. If there is substantial generalisation between all learning with human and robotic stimuli, then differences in associative learning cannot explain the human imitative bias.

However, the combination of findings in Experiments 6 and 7 provide good support for the ASL model of the human imitative bias as well as the ASL model of imitation, and it is difficult to reconcile these findings with a different hypothesis. The theoretical difference between Experiments 6 and 7 concerns whether it is possible to explain the influences of training with formation of short-term associations; it is possible to explain the influences of training in Experiment 6 in such a way but not the influences of training in Experiment 7. The empirical difference between Experiments 6 and 7 concerns whether training also influenced automatic imitation of human stimuli; Experiment 7 observed such an influence, but Experiment 6 did not. To suggest that the combination of results in Experiments 6 and 7 do not support the ASL hypothesis of the human imitative bias would require suggesting that the difference between Experiments 6 and 7, namely the lack of modulation of automatic imitation of human stimuli in Experiment 6, is due to formation of short-term associations. This argument is not very persuasive. It is therefore likely that the influences of training observed in Experiment 6 reflect formation of long-term associations in the same way as the influences of training observed in Experiment 7, and the substantial generalisation of training to human stimuli in Experiment 7 reflects acquired equivalence and the specific training paradigm employed (as discussed in section 4.3.3). These findings in combination are therefore more consistent with the ASL predictions of the human imitative bias than the AIM predictions.

Conclusion: The experiments reported within this chapter have suggested that automatic imitation of robotic stimuli increases following compatible training with those stimuli, relative to incompatible training, and that these effects are more likely to reflect formation of long-term associations established on the basis of practice during training, than short-term associations established on the basis of instructions given prior to training. The experiments have also suggested that this training can modulate the human imitative bias, such that compatible training will reduce the human imitative bias, relative to incompatible training. These findings are consistent with the ASL model of imitation, and not the AIM model.

Chapter 5: The role of experience in visuotactile integration

The experiments reported in Chapter 4 provided evidence that opportunities for associative learning can modulate imitation of non-human stimuli. The experiment reported here in Chapter 5 investigates whether opportunities for associative learning may similarly modulate visuotactile integration, that is, integration of visual and tactile representations of events. It also investigates whether any modulations are influenced by the identity of the stimulus, namely whether the visual stimulus is or is not human.

Two important parallels can be drawn between visuotactile integration and imitation. First, like imitation, visuotactile integration poses a correspondence problem. Patterns of stimulation on the retina and receptors on the skin would appear to be in incommensurable codes, and these codes must be integrated. Second, as in imitation, human stimuli appear to be especially potent in relation to visuotactile integration; human stimuli evoke greater visuotactile integration than non-human stimuli (Thomas, Press, & Haggard, 2006; Blakemore, Bristow, Bird, Frith, & Ward, 2005; Fiorio & Haggard, 2005; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Taylor-Clarke, Kennett, & Haggard, 2004; Taylor-Clarke, Kennett, & Haggard, 2002; Kennett, Taylor-Clarke, & Haggard, 2001; Graziano, Cooke, & Taylor, 2000; Pavani, Spence, & Driver, 2000). For example, Taylor-Clarke et al. (2004) found that participants were better able to determine the orientation of gratings presented to their fingertip when concurrently observing their hand, rather than a neutral object reflected into the same spatial location. Therefore, the necessity that imitation mechanisms and visuotactile integration mechanisms must both resolve the correspondence problem, and the fact that human stimuli appear especially potent with respect to operation of both mechanisms, may mean that similar theories can be used to understand visuotactile integration and imitation.

There is much evidence, both behavioural and neurological, that visual and tactile representations of events are integrated. At the behavioural level, visual stimuli presented near tactile targets increase the speed and accuracy with which those targets are detected (e.g. Ladavas, Farnè, Zeloni, & di Pellegrino, 2000; Driver & Spence, 1998; Ladavas & di Pellegrino, 1998; Spence, Nicholls, Gillespie, & Driver, 1998). These behavioural effects may be mediated by integration of visual and tactile modalities in the premotor and parietal cortex. Cells have been found in the premotor cortex and parietal lobule of the macaque monkey which are activated not only when a monkey is touched on the arm, but also when a visual stimulus is presented near the arm (e.g. Obayashi, Tanaka, & Iriki, 2000; Graziano, Yap, & Gross, 1994). Imaging studies have indicated that premotor and parietal cortices are also activated by both visual and tactile stimuli in humans (e.g. Saito, Okada, Morita, Yonekura, & Sadato, 2003; Banati, Goerres, Tjoa, Aggleton, & Grasby, 2000).

In addition, there is evidence that processing of visual stimuli in visual cortices is enhanced by the concurrent presence of touch (e.g. Kennett, Eimer, Spence, & Driver, 2001), and processing of tactile stimuli in somatosensory cortices is enhanced by the concurrent presence of visual stimuli (Fiorio & Haggard, 2005; Forster & Eimer, 2005; Taylor-Clarke et al., 2002). For example, Kennett et al. (2001) observed that occipital N1 components were larger in response to visual stimuli if tactile stimuli had preceded these visual stimuli on the same side, rather than the opposite side, of space.

Keysers et al. (2004) propose that the integration of vision and touch may arise through Hebbian learning. They state (p.341) 'when we observe ourselves being touched, the activation of somatosensory neurons will overlap in time with the activation of visual neurons that represent the visual stimulus of the touching event. Hebbian learning rules predict that this correlation in time should lead to strengthening of the synapses between these neurons.' The authors therefore propose that bimodal visuotactile cells are not bimodal at birth, but rather become bimodal through Hebbian learning. This hypothesis is consistent with evidence that somatosensory cells in the monkey will fire in response to visual stimuli only if these stimuli were previously paired with tactile information (Zhou & Fuster, 1997; 2000).

As far as I am aware, no one has explicitly suggested that visuotactile integration mechanisms are innate. However, this possibility was raised by the philosopher Locke, under the influence of his friend Molyneux (Locke, 1690). Molyneux's famous question asked whether a person born blind and able to discriminate cubes from spheres haptically, would be able to discriminate these shapes visually if their sight were suddenly restored. Several patient studies have attempted to answer this question (e.g. Ackroyd, Humphrey, & Warrington, 1974; Gregory & Wallace, 1963), and have found conflicting results. Upon finding some evidence to suggest that such a patient *was* able to discriminate shapes visually, Gregory & Wallace (1963) advanced an apparently nativist view: 'the fact that our patient was able, certainly with a minimum of training - and perhaps with none at all - to recognise by vision upper case letters which he had learned by touch...provides strong evidence for (non-learned) crossmodal transfer' (p.40).

Several studies have investigated the influence of training on visuotactile integration. These studies have investigated an interesting consequence of visuotactile integration, namely that when participants observe stimulation on a rubber hand while feeling stimulation on their own hand, they start to feel as if the rubber hand is their own hand (measured through self-report, Ehrsson, Spence, & Passingham, 2004; Armel & Ramachandran, 2003; Botvinick & Cohen, 1998). This 'rubber hand illusion' (RHI) is absent when seen and felt stimulation is out of phase (Ehrsson et al., 2004; Botvinick & Cohen, 1998) or when felt stimulation is presented randomly with respect to seen stimulation (Armel & Ramachandran, 2003). Converging evidence that the RHI results from visuotactile integration is provided by the finding that when participants are experiencing this illusion, they exhibit greater activation in the areas of premotor cortex where bimodal visuotactile cells have been found in primates (Ehrsson et al., 2004). Schaefer and colleagues (Schaefer, Noennig, Heinze, & Rotte, 2006) have also found that visuotactile integration processes which may give rise to the illusion can influence early sensory processing. The authors required participants to observe stimulation on a thumb while feeling stimulation on their own little finger. Using neuromagnetic source imaging, they found that synchronous stimulation of this kind resulted in a change in the location of the representation of the little finger in primary somatosensory cortex (SI). This was not the case when visual and tactile events were presented out of phase.

These studies therefore provide evidence of an influence of experience on visuotactile integration. Further studies suggest that influences of training on visuotactile integration depend on the type of visual stimulus presented, and specifically on whether the visual stimulus is or is not human. Tsakiris & Haggard (2005) measured the RHI with proprioceptive drift towards the observed stimulus. They found that, following synchronous stimulation of the participants' own left hand and a left rubber hand, participants perceived their own hand as closer to the rubber hand, relative to conditions where visual and tactile stimulation was asynchronous. In contrast, there was no difference in proprioceptive drift following synchronous and asynchronous stimulation of the participants' own hand and a wooden stick.

However, Armel & Ramachandran (2003) have not found an influence of visual stimulus type on the RHI. They stroked a rubber hand or the table top synchronously with the participant's own unseen hand, and subsequently measured skin conductance response when a finger was pulled back on the rubber hand or a plaster was pulled off the table top. They compared synchronous stimulation conditions where the participants could not see their own hand against control conditions where stimulation was still synchronous but participants could see their own hand; a condition which the authors felt would not give rise to the RHI. The authors found greater evidence of the RHI when participants viewed a rubber hand or a table top being stimulated synchronously with their own unseen hand, compared with control conditions, and this difference between test and control conditions was equal with the two visual stimulus types.

Therefore, previous research provides some support for the hypothesis that visual and tactile inputs *can* become integrated through associative learning. However, whether influences of training are dependent on whether the visual stimulus is or is not human is still a matter of debate. Tsakiris & Haggard (2005) suggest that differences as a function of visual stimulus identity are driven by the role of pre-existing body representations, and therefore that opportunities for learning cannot sufficiently explain integration effects. However, it is also possible that pre-existing body representations could be formed through previous associative learning experiences. It is likely that there are more opportunities for associative learning with human stimuli, relative to non-human stimuli. There will be plenty of opportunities provided during life to observe a body part whilst also feeling touch on that body part. For example, touch on a body part will often make one look towards that body part. In addition, in order to coordinate movement one will observe a moving body part and will often receive tactile stimulation on that body part by virtue of the movement, for example, when picking up a cup. One will look less frequently towards non-human stimuli when receiving tactile stimulation, providing fewer opportunities for associative learning between non-human visual stimuli and tactile representations of the body.

The purpose of Experiment 8 was not to investigate whether the differences observed by Tsakiris & Haggard (2005) with human and non-human stimuli result from previous associative learning experiences, but rather to further test whether influences of training on visuotactile integration depend in any way on whether visual stimuli are human or non-human. Such investigations can elucidate whether theories of visuotactile integration are required to explain the influence of the identity of visual stimuli on the effect of visuotactile training. Experiment 8 therefore used event-related brain potentials (ERPs) to investigate the influence of synchronous and uncorrelated visuotactile training with human and non-human visual stimuli on somatosensory processing. Greater visuotactile integration was expected to be reflected by enhanced somatosensory ERP components in response to tactile stimuli. In addition, any effects on later post-perceptual processes were investigated by analysing longer-latency ERP modulations.

During training phases, participants observed a left or right rubber hand (View Hand group) or a lateralised neutral object (View Object group) being tapped synchronously or randomly with respect to one of their own unseen hands. Participants were always stimulated on the hand which was compatible with that which they observed (or a spatially matched object). Thus, if they observed stimulation of a left stimulus, they were stimulated on their left hand, and if they observed stimulation of a right stimulus, they were stimulated on their right hand. ERPs elicited in response to mechanical vibratory tactile stimuli presented to both left and right hands were subsequently recorded (test phase). Therefore, in the test phase, ERPs triggered by tactile stimuli which were compatible with the viewed stimulus (compatible hand) could be compared with ERPs triggered by tactile stimuli which were incompatible with the viewed stimulus (incompatible hand). To ensure that participants paid attention to the stimulus display, they were required to observe and monitor an LED on the hand or object stimulus (see methods).

This procedure allowed investigation of any influences of the relationship between visual and tactile stimuli during the training phase on processing of tactile stimuli during the test phase, by comparing somatosensory processing following blocks where visuotactile stimulation had been synchronous and uncorrelated. It also allowed investigation of whether the type of visual stimulus (human or non-human) mediated influences of training. If visuotactile integration depends solely on innate mechanisms, somatosensory processing should be equal following synchronous and uncorrelated stimulation in both View Hand and View Object groups. In contrast, if visuotactile integration depends on learned mechanisms, somatosensory processing should be enhanced following synchronous, relative to uncorrelated, stimulation conditions. If there is an additional influence of whether the visual stimulus is or is not human, the influence of training on somatosensory processing may differ in View Hand and View Object groups.

5.1 Experiment 8

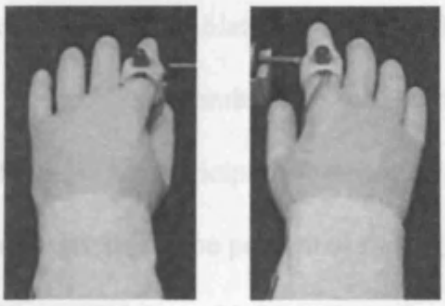
5.1.1 Method

Participants

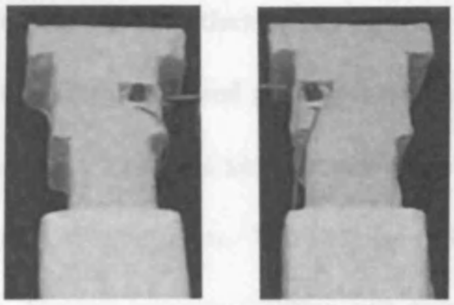
Thirty-five consenting, healthy volunteers with an average age of 27.0 years, 16 male, participated in Experiment 8, and were paid a small honorarium for their participation. Two participants were excluded due to insufficient eye movement control (see below), and one other participant was excluded due to excessive alpha activity. The remaining 32 participants were randomly assigned in equal numbers to the View Hand and View Object groups.

Stimuli

Experimental blocks consisted of sequential training and test phases. Throughout all blocks, participants viewed one of the four visual stimulus arrays depicted in Figure 20. The visual stimulus in the View Hand group consisted of either a left or right stuffed yellow rubber glove (extreme point length = 31.0°, extreme point width = 22.6°, sleeve of 15.9° width and 16.7° length), with an LED (target stimulus) wrapped around its index finger on the 'proximal' segment. The visual stimulus in the View Object group consisted of a symmetrical stuffed yellow rubber block, which was matched to the hand stimulus in extreme point dimensions, surface area and luminance, with LED location spatially matched to the position on the hand stimuli. The LED diameter was 2.30° and the luminance, measured with a SpectraScan PR650 luminance meter (Micron Techniques Ltd.) at a distance of 25 cm from the LED was 84 cd/m^2. Non-target LED flashes were of 200ms duration with no gap. Target LED flashes were of the same duration, but had a 30ms gap in the middle i.e. on for 85ms, off for 30ms, then on again for 85ms. All visual stimulus displays also contained a red wooden stick (6.9° long) which tapped the hand or object stimulus for 50ms during training phases on the middle segment of the index finger on the hand stimulus or on the spatially matched location on the object stimulus.



A Left hand **B Right hand**



C Left object **D Right object**

Figure 20: The stimuli used in Experiment 8. A Left hand, B Right hand, C Left object, D Right object.

Tactile stimuli were presented using 12V solenoids, driving a metal rod with a blunt conical tip, making contact with the fingers or the rubber stimuli whenever a current was passed through the solenoid. During the training phases, single taps of 50ms duration were presented to the outer side of the middle segment of the index finger of the hand corresponding to the viewed rubber stimulus (i.e. left hand stimulation with left rubber hand or object; right hand stimulation with right rubber hand or object). During the test phase, vibratory stimuli were delivered to the distal pad of the left or right index fingers. These stimuli had a frequency of 50Hz and were of 102ms duration (created by switching solenoids on for 2ms and off for 18ms six times).

Procedure

Participants were tested individually in a dimly lit room. Participants' right and left hands were placed palm-side down on a tabletop 17.5cm to the right and left of the body midline (see Figure 21). The rubber stimulus was positioned such that the LED was aligned with the body midline. The participants' index fingers were resting in plastic casing, within which the tactile stimuli to be presented during test phases were embodied. A black frame (Width = 85cm, Height = 11.5cm, Length = 40cm) was placed on the tabletop so that participants could not see their hands and the tactile stimulators. A 57.0° x 22.8° hole in the top of this frame allowed participants to see the stimulus display. A black cloth was attached to the frame and tied around the participants' necks such that they could not see the location of their arms. White noise (78 dB SPL) was continuously presented via a loudspeaker located at body midline and directly behind the black frame to mask any sound produced by the tactile stimulators.

Each block consisted of three rotations of training and test phases (training phase followed by test phase). During training phases, viewed taps on the rubber stimulus and felt taps on the spatially corresponding hand were presented either synchronously or in an

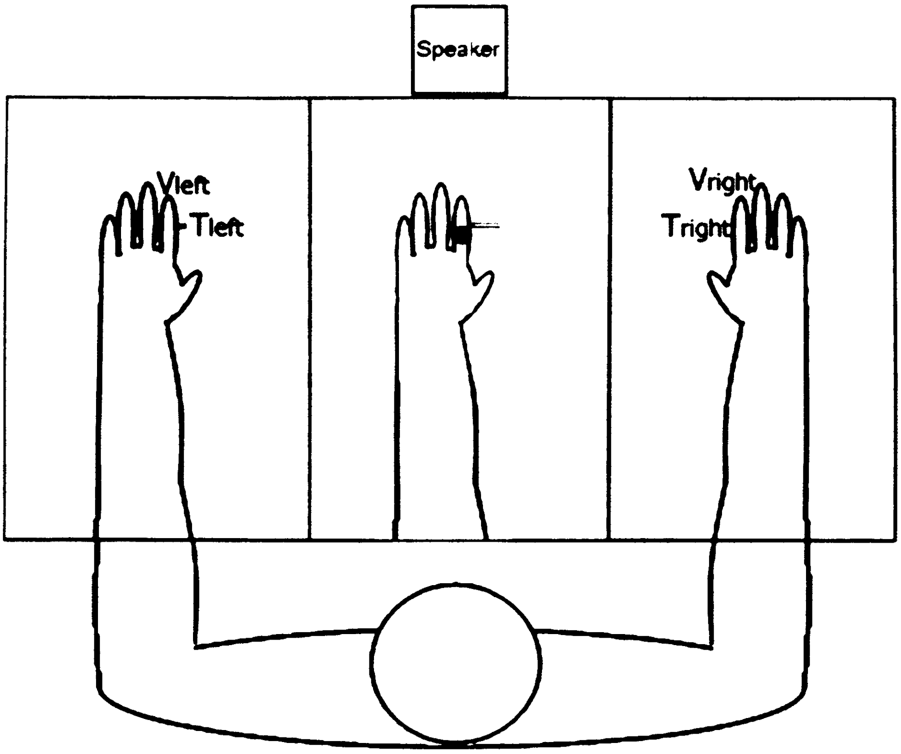


Figure 21: Experiment 8. Experimental set-up. The left hand stimulus for participants in the View Hand group is represented within the white square. The participants' own hands were out of sight for the duration of the experiment. In training phases, the participant received taps to the side of the middle segment of their index finger that was congruent with the viewed stimulus (Tleft or Tright). In test phases, the participant received vibrations to both fingertips (Vleft or Vright).

uncorrelated fashion. Each 'trial' in training phases consisted of presentation of both visual and tactile stimuli and lasted for 1300ms. In synchronous blocks, visual and tactile stimuli were presented simultaneously, at one of 13 possible time points between 0ms to 1200ms after training trial onset in 100ms steps (0ms, 100ms, 200ms, to 1200ms). In uncorrelated blocks, visual and tactile stimuli were also presented at one of these time points, but the point at which the tactile stimulus was presented was random with respect to the point at which the visual stimulus was presented.

Test phases following synchronous and uncorrelated training were identical; vibratory stimuli were presented with equal probability to the left and right hands, in a random order, with an inter-trial interval varying between 1000ms and 1400ms (mean = 1200ms). There was no stimulation of the seen rubber stimulus during these phases. The different combinations of training and test phases are indicated in Table 2.

	Viewed stimulus type (training and test)	**Stimulated hand (training)**	**Stimulation type (training)**	**Stimulated hand (test)**
Right-Synchronous condition	Right	Right	Synchronous	Right and left
Left-Synchronous condition	Left	Left	Synchronous	Right and left
Right-Uncorrelated condition	Right	Right	Uncorrelated	Right and left
Left-Uncorrelated condition	Left	Left	Uncorrelated	Right and left

Table 2: Experiment 8. A table of conditions, according to the combination of within-subject variables of viewed stimulus type in training and test phases, stimulated hand and stimulation type in training phases and stimulated hand in test phases. Those participants in the View Hand and View Object groups all undertook these conditions with either a Hand or Object stimulus, respectively.

During both training and test phases, the participants' task was to watch the LED located on the rubber stimulus and to say 'yes' whenever they detected an LED flash with a gap. They were instructed to refrain from responding when they detected an LED flash without a gap, or when any other stimuli were presented. Participants wore a head-mounted microphone to detect vocal responses. LED trials were placed with equal frequency in training and test phases, and consisted of a target or non-target LED flash, followed by a 1000 - 1400ms (mean = 1200ms) interval to allow participants to respond (or not). No additional visual and tactile stimuli were presented during LED trials.

Each training phase presented, in random order, 26 visual/tactile trials, two LED target trials and two LED non-target trials. Each test phase presented, in random order, 13 left vibration stimuli, 13 right vibration stimuli, two LED target trials and two LED non-target trials.

There were three blocks of each type, defined by combination of rubber stimulus lateralisation (left and right) and training type (synchronous and uncorrelated), and these were completed in immediate succession. Those blocks of the same training type were completed consecutively, and rubber stimulus lateralisation was ordered in an ABBA fashion. The order of blocks distinguished by rubber stimulus lateralisation and training type was counterbalanced. Before testing commenced in each new condition, participants completed one training block of 60 trials that consisted of one training phase followed by one test phase.

EEG recording and data analyses

EEG was recorded with Ag-AgCl electrodes and linked-earlobe reference from FPz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, and Oz (according to the 10-20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal electro-oculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5kΩ, and the impedances of the earlobe electrodes were kept as equal as possible. Amplifier bandpass was 0.1 to 40 Hz. EEG and EOG were sampled with a digitization rate of 200 Hz and stored on disk.

EEG and EOG for test phase trials were epoched off-line into 600 ms periods, starting 100ms prior to tactile stimulus onset and ending 500 ms after onset. Trials immediately following those where a target LED was presented were excluded to avoid contamination by vocal responses. Trials with vocal responses to tactile stimuli were also excluded from EEG analysis, as were non-target trials with eyeblinks (FPz exceeding ±60 μV), small horizontal eye movements (HEOG exceeding ±30 μV), or other artifacts (a voltage exceeding ±80 μV at any electrode) in the interval between tactile stimulus onset and 500 ms after. Averaged HEOG waveforms obtained for each participant and task condition in this interval in response to left versus right hand stimuli were scored for systematic deviations of eye position, which indicate residual tendencies to move the eyes towards the stimuli. Two participants were excluded because residual HEOG deviations exceeded ±3μV.

The EEG obtained in the 500ms interval following tactile stimulus onset for each participant in the View Hand and View Object groups was averaged relative to a 100ms pre-stimulus baseline for all combinations of stimulated hand (left and right), training type (synchronous and uncorrelated) and visuotactile compatibility (compatible and incompatible, where compatible = left hand stimulation when viewing a left rubber stimulus and right hand stimulation when viewing a right rubber stimulus, and incompatible = left and left, right and right, and incompatible = left hand stimulation when viewing a right rubber stimulus and right hand stimulation when viewing a left rubber stimulus). ERP mean amplitudes were computed within measurement windows centered on the latency of somatosensory P50 (30-65 ms), N80 (65-90 ms), P100 (90-115 ms) and N140 (120-160 ms) components, as well as within a longer-latency time window (200-450 ms post-stimulus). Analyses of ERP data were conducted for lateral recording sites where the amplitudes of early somatosensory components are maximal (F3/4, FC5/6, C3/4, and CP5/6), as well as for midline electrodes (Fz, Cz, and Pz).

5.1.2 Results

Behavioural performance

The RT and error data (failure to respond) for visual targets were subjected to ANOVA in which training type (synchronous and uncorrelated) and phase of experiment (training and test) were within-subject variables. Stimulus type (View Hand and View Object) was a between-subject variable. There were no significant main effects or interactions in either of these analyses. Participants in the View Hand group had similar mean RTs and error rates (592ms, 4.5%) to participants in the View Object group (582.2ms, 4.5%). Mean RTs and error rates were also similar in synchronous (588.1ms, 4.8%) and uncorrelated stimulation conditions (582.1ms, 4.2%). This suggests that participants were equally attentive in all conditions and in both groups. Participants made vocal responses in 1.3% of visual non-target trials. These data were not analysed further.

ERPs to vibratory tactile stimuli presented in the test phase

Figure 22 represents ERPs elicited at midline electrode Cz and at electrodes C3/C4 ipsilateral and contralateral to the stimulated hand, collapsed across visuotactile compatible and incompatible trials. There is a notable enhancement of the amplitude of the somatosensory N140 component in blocks where training had been synchronous,

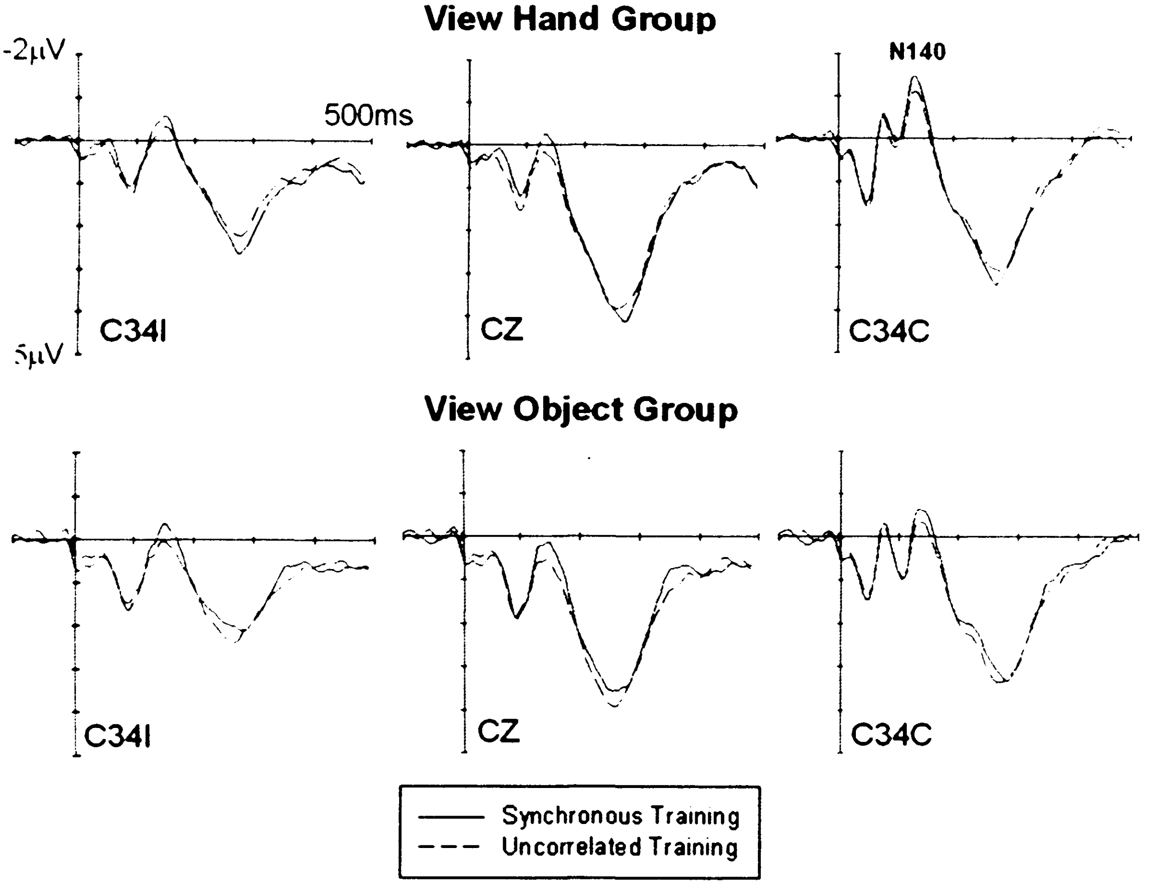


Figure 22: Experiment 8. Grand-averaged ERPs elicited in response to tactile stimuli delivered in test phases in the 500 ms interval after tactile stimulus onset at midline electrode Cz, and at central electrodes C3 and C4 ipsilateral (C34I) and contralateral (C34C) to the stimulated hand. ERPs are shown separately for the View Hand group (top panel) and the View Object group (bottom panel), and for blocks with synchronous visuotactile training (solid lines), and blocks with uncorrelated training (dashed lines).

relative to blocks where training had been uncorrelated, and this modulation was no different in the View Hand and View Object groups. These observations were substantiated by statistical analysis. The data were subjected to two sets of ANOVAs, one for lateral electrodes and one for midline electrodes, within measurement windows centered on P50, N80, P100 and N140 components, as well as within a longer-latency time window (200-450 ms post-stimulus). The lateral analyses contained within-subject variables of laterality (contralateral and ipsilateral) and electrode (F3/4, FC5/6, C3/4 and CP5/6), and a between-subject variable of stimulus type (View Hand and View Object). The midline analysis contained no laterality variable, and the electrode variable had only three levels (Fz, Cz and Pz). In the N140 time window (120-160ms after stimulus onset), there was a main effect of training type, which was reliable both in the lateral ($F(1,30) = 6.8$, $p < 0.02$), and the midline analyses ($F(1,30) = 7.7$, $p < 0.01$). This main effect was independent of whether the seen visual stimulus was a rubber hand or object in both lateral and midline analyses ($F < 1$ in both cases). The analyses indicated no reliable effects of training in the P50, N80 or P100 time ranges, or 200-450 ms post-stimulus.

Figure 23 represents ERPs elicited at midline electrode Cz and at electrodes C3 and C4, ipsilateral and contralateral to the stimulated hand, in response to tactile stimuli delivered in test phases where tactile stimuli were compatible or incompatible with the visual stimulus. There are observable differences in the 200-450ms interval. There is an observable enhanced negativity in response to tactile stimuli which were presented to the hand which was compatible with the rubber stimulus, compared with stimuli which were presented to the incompatible hand. This was the case with both synchronous and uncorrelated training types in the View Object group, but only with synchronous training the View Hand group. These observations were supported by statistical analysis. Within the time interval 200-450ms after stimulus onset, there was first, a significant main effect of visuotactile compatibility (lateral: $F(1,30) = 13.3$, $p < 0.002$, midline: $F(1,30) = 11.0$, $p < 0.005$), and second, a significant visuotactile compatibility x training type x stimulus type interaction (lateral: $F(1,30) = 6.3$, $p < 0.02$, midline: $F(1,30) = 5.5$, $p < 0.03$). There was no evidence of a main effect of visuotactile compatibility in the View Hand group (lateral: $F(1,15) = 1.9$, $p = 0.2$, midline: $F(1,15) = 1.2$, $p = 0.3$), but there was a two-way interaction between visuotactile compatibility and training type (lateral: $F(1,15) = 6.2$, $p < 0.03$, midline: $F(1,15) = 9.7$, $p < 0.01$). This two-way interaction was generated by an effect of visuotactile compatibility with synchronous training (lateral: $F(1,15) = 8.4$, $p <$

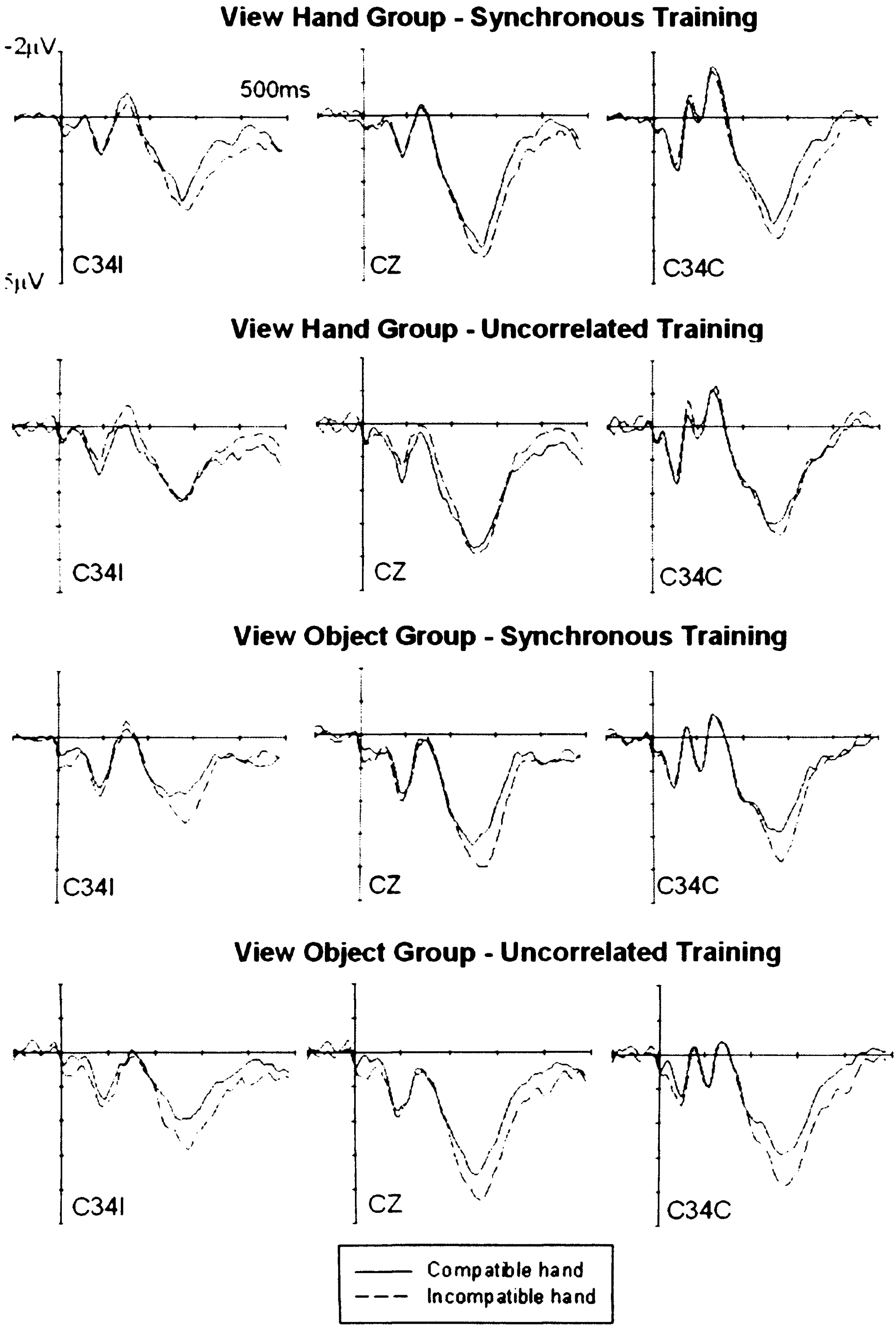


Figure 23: Experiment 8. Grand-averaged ERPs elicited in response to tactile stimuli delivered in test phases in the 500 ms interval after tactile stimulus onset at midline electrode Cz, and at central electrodes C3 and C4 ipsilateral (C34I) and contralateral (C34C) to the stimulated hand. ERPs are shown separately for the View Hand and View Object groups, and for blocks with synchronous and uncorrelated training. ERPs on trials where the stimulated hand was compatible with the seen rubber object (solid lines) are compared to ERPs on trials where tactile stimuli were presented to the incompatible hand (dashed lines).

0.02, midline: $F(1,15) = 11.1$, $p = 0.005$), but not with uncorrelated training ($F < 1$ in both cases). In contrast, the View Object group displayed a main effect of visuotactile compatibility (lateral: $F(1,15) = 16.3$, $p < 0.002$, midline: $F(1,15) = 17.9$, $p = 0.001$), but no evidence of a two-way interaction between visuotactile compatibility and training type (lateral: $F(1,15) = 1.4$, $p = 0.3$, midline: $F < 1$). There were no main effects or interactions involving visuotactile compatibility in the P50, N80, P100 and N140 timeranges.

5.1.3 Discussion

Experiment 8 explored the role of experience and stimulus identity in visuotactile integration, assessing first, whether visuotactile integration can be modulated through training, and second, whether these modulations are dependent on the identity of the visual stimulus (human or non-human). A procedure was employed whereby participants observed a rubber hand (View Hand group) or neutral object (View Object group) being stimulated synchronously or randomly with respect to their own unseen hand. Subsequent to these training phases, somatosensory ERPs were measured in response to tactile stimuli, and greater visuotactile integration was expected to be reflected by enhanced somatosensory processing of these tactile stimuli.

The results indicated that the N140 component of somatosensory processing is enhanced following synchronous stimulation of a hand or object stimulus and the participant's own hand, relative to uncorrelated stimulation conditions. There was no influence on the N140 component of whether the visual stimulus was a hand or object. There was also no interaction between training type and visuotactile compatibility, indicating that somatosensory processing of stimuli presented to the hand which was incompatible with the visual stimulus was also influenced by training. This finding is consistent with the known bilaterality of secondary somatosensory cortex (SII, Hari et al., 1984), where the N140 component is thought to be generated (Allison, McCarthy, & Wood, 1992).

These findings suggest that tactile processing in SII can be modulated by visuotactile associative learning. The finding that, specifically, processing in somatosensory cortex can be modulated by training is consistent with previous findings (Schaefer et al., 2006), although previous studies have found modulations in SI rather than SII. This pattern of results is inconsistent with the hypothesis that visuotactile integration is mediated by innate mechanisms, which would have predicted no modulation of ERPs as a function of whether stimulation was synchronous or uncorrelated.

If one assumes that the modulations observable on the N140 component in Experiment 8 reflect operation of the same visuotactile integration mechanisms as those which generate the RHI, the finding that these modulations are independent of the identity of visual stimuli is consistent with the findings of Armel & Ramachandran (2003) that the RHI is independent of the identity of visual stimuli. This finding is less consistent with those of Tsakiris & Haggard (2005), which indicate that the RHI is generated with rubber hands but not neutral objects.

However, the findings of Tsakiris & Haggard (2005) may be interpretable in the light of the modulations observed 200-450ms post-stimulus. In this time interval, there was an enhanced negativity for stimuli presented to the hand which was compatible with the visual stimulus, compared with stimuli presented to the hand which was incompatible.

This effect was present in both synchronous and uncorrelated training conditions in the View Object group, but only in the synchronous training condition in the View Hand group.

A sustained negativity in somatosensory ERPs beyond 200ms post-stimulus is usually interpreted as evidence of enhanced attention towards those stimuli, such that those stimuli are processed at greater depth (e.g. Eimer & Forster, 2003; Michie, 1984). Thus, the presence of such a sustained negativity on compatible compared with incompatible trials may indicate that vision of a left or right rubber stimulus resulted in an attentional bias towards the hand compatible with this stimulus. Such a bias is likely to result from the association of the lateralised features of the rubber stimulus with the side of tactile stimulation during training (e.g. viewing a left rubber stimulus is associated with tactile stimulation of the participant's left hand). The observation that no such enhanced negativity for compatible trials was observed in the View Hand group following uncorrelated training suggests that there was no attentional bias towards the compatible hand in this condition, and might be explained with reference to pre-existing body representations involving hand stimuli. These pre-existing representations may result in strong expectations of correlated visual and tactile events. The View Hand group may therefore learn very rapidly in the uncorrelated stimulation condition that these expectations have not been met, because surprise leads to rapid learning (Schultz & Dickinson, 2000). If participants learn very quickly in this condition, this may prevent any subsequent attentional bias towards the compatible side because participants will not continue to establish the relationship between visual and tactile events in this condition.

According to this post-hoc account, the identity of the visual stimulus may indeed have interacted with the influence of training on visuotactile integration. This may provide an explanation of the observation by Tsakiris & Haggard (2005) that the RHI is dependent on the identity of the visual stimuli in two ways. First, Tsakiris & Haggard (2005) only presented four minutes of training in each condition, and it was suggested, on the basis of the late attentional modulation, that participants learn faster in the hand asynchronous condition relative to other conditions because of high surprise. Therefore, given that very little training was presented, the influence of training may only have been observed in hand stimulation conditions. If more training had been presented, influences may also have been observed in object stimulation conditions. Second, it was hypothesised that participants learnt faster in the hand asynchronous condition because there was not the same attentional bias towards the tactile stimuli involved in training which was observable in the other conditions. If participants were not paying attention to the same point in space in the hand asynchronous condition, relative to the other conditions, participants may have given different estimates of the location of their hand. It is likely that estimates of the location of ones hand are influenced by the attentional focus of participants in addition to visuotactile integration.

Conclusion: Experiment 8 has suggested that visuotactile experience can modulate SII processing of tactile events independently of whether visual stimuli are human or non-human. However, ERP modulations observed beyond 200ms post-stimulus, which suggest attentional biases induced by visuotactile training, were influenced by whether the visual stimulus was human or non-human. It therefore appears that training can influence visuotactile integration, but there are some differences in influences of training with human and non-human visual stimuli. These differences may emerge through pre-existing body representations which exist with human stimuli and not non-human stimuli.

Chapter 6: General discussion

Contents

6.1 Overview

This chapter will summarise the findings from Experiments 1 - 8 with reference to the theoretical questions which they investigated. The findings from experiments in each chapter will be outlined, along with likely interpretations of the findings. Following these summaries, the limitations of the experiments will be discussed, along with the questions which still need to be addressed. Section 6.2 will review Experiments 1 and 2 (Chapter 2), which assessed whether compatibility effects generated with hand opening and closing movements are likely to reflect configural action compatibility or orthogonal spatial compatibility. Section 6.3 will review Experiments 3 and 4 (Chapter 3) which addressed whether a human imitative bias may be mediated by top-down processes, operating on the basis of knowledge about stimulus identity, or bottom-up processes, operating on the basis of perceptual properties of the stimuli. Section 6.4 will review Experiments 5 - 7 (Chapter 4) which investigated whether automatic imitation of non-human stimuli and hence the human imitative bias could be modulated through experience. This section will be the most substantial because these experiments were of greatest theoretical interest. Section 6.5 will review Experiment 8 (Chapter 5) which explored whether visuotactile integration could be modulated through experience, and the dependency of any influences on whether the visual stimuli were human or non-human. Finally, section 6.6 presents likely conclusions from the experiments reported in this thesis.

6.2 Configural action compatibility or orthogonal spatial compatibility?

6.2.1 Summary and interpretation

Experiments 1 and 2 investigated whether compatibility effects observed with opening and closing hand actions, where stimulus and response hands are in orthogonal dimensions, are driven by configural action compatibility or orthogonal spatial compatibility. If the effects are driven by configural action compatibility they should be determined by whether the stimulus and response hands are opening (configurally, the fingers move outwards) or closing (configurally, the fingers move inwards). If the effects are driven by orthogonal spatial compatibility they should be determined by whether the response fingers move up or down in response to stimulus fingers moving to the left or right.

Experiment 1 distinguished these hypotheses by investigating whether compatibility effects remained the same or reversed when stimulus movement direction reversed, by presenting participants with right stimulus hands viewed from the front (thumb on the left when fingers point upwards) and viewed from the rear (thumb on the right when fingers point upwards). Compatibility effects were found to remain the same when stimulus movement direction reversed. Experiment 2 similarly investigated whether compatibility effects remained the same or reversed when stimulus movement direction reversed, but compared compatibility effects between stimuli where configural action compatibility and orthogonal spatial compatibility were varied on entirely independent dimensions. This was achieved by taking one set of stimuli and flipping them in a vertical axis to create stimuli with opposite movement directions. In addition, this experiment investigated whether there were different spatial preferences in right and left hemispace, because orthogonal spatial compatibility effects have been found to differ in the two hemispaces. Similarly to Experiment 1, Experiment 2 found that compatibility effects remained the same regardless of stimulus movement direction. In addition, it found that compatibility effects did not demonstrate the interactions with response hemispace which have been found with some previous investigations of orthogonal spatial compatibility.

The findings within these experiments therefore suggest that compatibility effects observed with opening and closing hand actions are driven by configural action compatibility rather than orthogonal spatial compatibility. These findings suggest that actions can be represented configurally in imitation mechanisms. These experiments also indicate that these movements and this paradigm are appropriate for investigation of imitation mechanisms in this thesis.

6.2.2 Limitations and outstanding questions

By addressing which spatial codes may mediate action compatibility, interesting issues are raised concerning what constitutes an imitative response. It may be suggested that a perfect imitative response is only achieved if ones own body is aligned with that of an observed party; when the observed party lifts their left leg to their left side and we also lift our left leg to our left side, both legs will move in the same direction in space, defined in simple egocentric codes. However, it was noted in Chapter 2 that an action can still be considered an imitative response if ones own body is oriented differently to that of the observed party, and this may be considered just as perfect an imitative response as if bodies are oriented similarly. Concepts of match may depend only on some spatial codes and not others. Some behavioural and neurological research suggests that body orientation does not influence automatic imitation (e.g. Iacoboni, 2003), but other research suggests an influence (e.g. Aziz-Zadeh et al., 2002). Further research in this area may help clarify which spatial codes are important for automatic imitation. In addition, research into intentional imitation may inform understanding by investigating which rotations will make action more difficult to imitate and which rotations will result in rating an action as less imitative of another.

Experiments 1 and 2 have addressed the spatial codes which may drive action compatibility. However, it has already been noted in Chapters 3 and 4 that compatibility on other codes may also drive action compatibility. Compatibility of observed and executed actions on other perceptual features like skin folds and shading may also be important. In addition, temporal features of movement may drive action compatibility. This thesis has referred to the temporal features of movement in very general terms, for example, whether something moves up, down, left or right over time. However, more specific temporal features of observed and executed movement may also be encoded, and some have suggested that temporal features of both observed and executed movement are encoded in similar ways (e.g. Ivry & Hazeltine, 1995; Treisman, Faulkner, & Naish, 1992; Keele, Pokorny, Corcos, & Ivry, 1985). Therefore, it is possible that, in addition to compatibility on spatial codes, action compatibility is also driven by compatibility between observed and executed movement speeds. Future research could address this possibility.

6.3 Top-down and bottom-up contributions to the human imitative bias

6.3.1 Summary and interpretation

Experiments 3 and 4 investigated whether the human imitative bias is mediated by knowledge about stimulus identity (top-down influence) or properties of the stimuli (bottom-up influence). Experiment 3 presented participants with human stimuli and informed participants prior to one session of testing that stimuli were human, and prior to the other that they were robotic. Despite questionnaire responses indicating that the belief manipulation was successful, Experiment 3 did not detect a difference in automatic imitation of stimuli which participants had been instructed were human and stimuli which participants had been instructed were robotic. In a factorial design, Experiment 4 performed a further test of the top-down hypothesis, but also investigated bottom-up influences. Different participants were presented with genuinely human or genuinely robotic stimuli, and informed prior to one session that stimuli were human and prior to the other, that they were robotic. Similarly to Experiment 3, questionnaire responses indicated that the belief manipulation was successful, but an influence of belief on automatic imitation was not detected. However, an influence of perceptual properties was observed; the genuinely human stimuli evoked greater automatic imitation than the genuinely robotic stimuli.

The results of Experiments 3 and 4 therefore indicate that, in the case of opening and closing hand stimuli, the human imitative bias is driven by properties of the stimuli rather than beliefs about stimulus identity. This is consistent with hypotheses that processing within imitation mechanisms influences processing within higher level mechanisms involved in drawing mental state inferences (e.g. Kilner et al., 2003; Gallese & Goldman, 1998), because humans have mental states and robots do not. However, it is inconsistent with the converse hypothesis; that these higher level mechanisms modulate processing in imitation mechanisms, thereby producing a human imitative bias.

The interpretation that the human imitative bias is governed more by properties of the stimuli is consistent with both AIM and ASL models of imitation. The AIM model would predict that stimuli with human properties are allowed privileged access to an imitation module, and the ASL model would predict that stimuli with human properties are associated with matching responses more than stimuli with robotic properties.

6.3.2 Limitations and outstanding questions

In Experiments 3 and 4 the participants were simply instructed that the observed stimuli were human or robotic, and a questionnaire was used to assess whether the instruction manipulation was effective. As discussed in Chapter 3, questionnaire responses are susceptible to demand effects. However, two reasons were discussed why it is unlikely that the questionnaire measure used in these experiments was contaminated by demand effects. Despite these reasons, it remains a possibility that no top-down influence was observed on automatic imitation because participants' beliefs about stimulus identity did not actually differ as a function of instruction. It may therefore be informative to conduct an experiment which is similar to Experiment 4, but which has a measure of belief manipulation which is less susceptible to demand effects. For example, any measures of belief which do not require asking participants about their beliefs would be useful, but I have no suggestions at present concerning what these could be.

If the questionnaire measure in Experiments 3 and 4 accurately reflected participants' beliefs about stimulus identity, and therefore there is no top-down modulation of imitation on the basis of knowledge about stimulus identity with these movements and this task, these results do not exclude the possibility that there is top-down modulation on the basis of beliefs about identity in contrasting conditions. In Experiments 3 and 4, the movement stimuli were in full view, presentation of the human and robotic stimuli was blocked, and participants were not explicitly encouraged to think about the meaning of the observed movements or the intentions of the actor. These conditions resemble those in which a human imitative bias has been found previously and are not unusual in everyday life. However, knowledge about stimulus identity may have a larger influence on imitation if task requirements specify that participants should explicitly draw inferences about mental states underlying observed stimulus movements. In addition, knowledge about stimulus identity may have a larger influence on automatic imitation of other actions. For example, some actions, like facial expressions, may be especially important for higher sociocognitive functions. Therefore, there may be top-down influence of belief about identity on imitation of these actions.

As noted, the finding that the human imitative bias is driven by stimulus properties is consistent with hypotheses that processing within imitation mechanisms influences processing within higher level mechanisms involved in drawing mental state inferences. Several authors have suggested the involvement of imitation mechanisms in such higher level functions (e.g. Rizzolatti, 2005; Kilner et al., 2003; Gallese & Goldman, 1998). Although I have described such hypotheses as invoking imitation mechanisms which feed into higher level mechanisms, Gallese & Goldman (1998) and Rizzolatti (2005) in fact appear to posit that mental state inferences are drawn within imitation mechanisms themselves. For example, Rizzolatti (2005) suggests that actions which produce imitation without being understood rely on different mechanisms to those which produce imitation whilst being understood. This may reflect nothing more than a difference in terminology; Rizzolatti may view higher level mechanisms which receive input from imitation mechanisms as higher level imitation mechanisms. This is possible, although the specific relevance of these higher level mechanisms to imitation would require some clarification. Further investigation of influences which these higher-level mechanisms may have on imitation mechanisms would at least elucidate whether there is any relevance of these mechanisms to imitation, even if they are not directly implicated in solving the correspondence problem.

6.4 The role of experience in imitation of non-human stimuli

6.4.1 Summary and interpretation

Using a training paradigm with robotic stimuli, Experiments 5 – 7 aimed to distinguish AIM and ASL theories of a human imitative bias. Experiment 5 initially established a human imitative bias with stimuli which were suitable for use in a training paradigm. Experiment 6 investigated whether automatic imitation of robotic stimuli was greater following compatible training with these stimuli, relative to incompatible training. During training, one group of participants was instructed to perform movements which were compatible with those of a robotic stimulus and the other group was instructed to perform movements which were incompatible. This experiment found an influence of experience on automatic imitation of robotic stimuli; automatic imitation of robotic stimuli was greater following compatible training with the stimuli relative to incompatible training. The human imitative bias was therefore reduced with compatible training, relative to incompatible training.

Experiment 7 employed a similar training paradigm to Experiment 6, but did not refer to the stimulus-response relationship in the instructions given prior to training. This allowed investigation of whether the effects of training observed in Experiment 6 reflected formation of long-term associations, established on the basis of practice and postulated by the ASL model to mediate imitation, or formation of short-term associations, established on the basis of instructions given prior to training. In Experiment 7, participants were required to select their response on the basis of a number presented on the warning stimulus and to execute this response when an imperative stimulus posture was presented. In the compatible training group, this posture was the same as the required response, and in the incompatible training group, this posture was different to the required response. Despite no reference to the stimulus-response relationship in the task instructions given prior to training, automatic imitation of robotic stimuli was greater following compatible training with those stimuli, relative to incompatible training. Automatic imitation of human stimuli was also influenced by the training with robotic stimuli.

These findings indicate that automatic imitation of robotic stimuli is modulated by training, and that these modulations are more likely to reflect formation of long-term associations established on the basis of practice than short-term associations established on the basis of task instructions. These findings are consistent with the ASL model of imitation, which posits that imitation mechanisms are created through associative learning connecting visual and motor representations of action. The finding that automatic imitation of robotic stimuli can be modulated through experience, and that this modulation is likely to reflect formation of long-term associations, is inconsistent with the AIM model of imitation which proposes that imitation is mediated by innate mechanisms.

The ASL model predicts that the human imitative bias emerges through greater opportunities for associative learning connecting human movement stimuli and responses than non-human movement stimuli and responses. Providing opportunities for associative learning with non-human movement stimuli is therefore predicted to modulate the human imitative bias in addition to automatic imitation of robotic stimuli. Evidence consistent with this hypothesis was observed in Experiment 6, but not in Experiment 7. This was because training in Experiment 7 also influenced imitation of human stimuli, with which participants had not been trained. However, the combination of results in Experiments 6 and 7 are more consistent with the ASL predictions of the origin of a human bias, relative to the AIM predictions.

6.4.2 Limitations and outstanding questions

Experiment 7 observed the influence of training on automatic imitation of robotic stimuli which the ASL model would predict, but it did not observe the predicted influence of training on the human imitative bias because training also influenced imitation of human stimuli. Although the combination of results of Experiments 6 and 7 are difficult to reconcile with any hypotheses of the human imitative bias other than that of the ASL model, further work can be done to dissociate short- and long-term association hypotheses, and AIM and ASL hypotheses, of the influences of training on imitation. A further way in which short- and long-term association hypotheses could be dissociated would be to provide opportunities for formation of short-term associations, but to remove opportunities for formation of long-term associations. Participants could be given the instructions to perform responses which are compatible or incompatible with movements of robotic stimuli, but trials on which this behaviour is required could be omitted. If effects of training are still observed, this would suggest formation of short-term associations, rather than long-term associations. This hypothesis would not be inconsistent with either the AIM or the ASL model of imitation, because neither hypothesis denies an influence of task sets on behaviour. However, if effects of training are no longer observed, this may suggest that effects of training observed when participants have actually executed actions in response to stimuli, reflect formation of long-term associations. This outcome would be consistent with the ASL model of imitation, and not the AIM model.

An alternative or additional way in which short- and long-term association hypotheses, and therefore AIM and ASL hypotheses, can be distinguished would be to use a similar paradigm to Experiment 7 but to train participants with human stimuli rather than robotic stimuli. One of the possible explanations why training with robotic stimuli also influenced imitation of human stimuli in Experiment 7 is that human stimuli are already associated with compatible responses before training. When robotic stimuli are paired with compatible responses during training, this could strengthen compatible associations between human stimuli and responses in addition to associations between robotic stimuli and responses ('acquired equivalence'). Training with human stimuli could overcome this problem, because robotic stimuli are unlikely to be associated with compatible responses before training. Therefore, this procedure may mean that substantial generalisation of training is not observed and that the human imitative bias is modulated through training.

Short-term and long-term hypotheses may be dissociable on more dimensions than the conditions in which they are formed (practice or instructions). For example, short-term associations have been hypothesised to operate via frontal control mechanisms (e.g. Dove et al., 2000; Pollmann et al., 2000), whereas long-term associations have been hypothesised to be direct. Therefore, these hypotheses could be distinguished neurologically. Following training, participants could observe actions. If training has notable influences on cortical areas involved in frontal control, the short-term hypothesis may be correct. In contrast, if training has only notable influences on premotor areas, where motor representations of action are thought to be located, the long-term hypothesis may be correct. Second, Barber & O'Leary (1997) have suggested that short-term associations do not remain active after the task is complete, whereas long-term associations can have durable influences on behaviour. In this case, these hypotheses could be distinguished by noting whether training has observable influences on imitation following a longer period of time than 24 hours, for example, one week.

Third, short-term associations may operate only to inhibit incorrect responses, rather than to facilitate correct responses. When the frontal areas thought to mediate short-term associations were disrupted in rodents, the rodents performed more incorrect responses but the number of correct responses performed remained unchanged (de Wit, Kosaki, Balleine, & Dickinson, 2006). In contrast, long-term associations are thought to be both excitatory and inhibitory (e.g. Mackintosh, 1974). A short-term hypothesis may therefore suggest that differences between compatible and incompatible training groups are driven only by incompatible training, and that this influence is driven by facilitation of RTs on incompatible trials at post-test relative to pre-test. In contrast, a long-term hypothesis of influences of training would suggest that both compatible and incompatible training can influence behaviour. It may therefore be possible to distinguish these hypotheses by designing a training experiment where effects of compatible training can be dissociated from effects of response practice and perceptual learning, but without comparing effects with those of incompatible training. For example, participants could practise responses and observe stimuli to the same extent as a compatible training group, but these tasks could be performed in separate blocks. If there is an observable influence of compatible training, this may provide evidence in support of the long-term hypothesis.

Experiments 6 and 7 investigated whether automatic imitation of robotic stimuli could be modulated through training in order to contrast AIM and ASL theories of imitation and the human imitative bias. However, a defender of AIM might argue that automatic imitation cannot be used as a test bed for this theory because AIM relates, not to unintentional imitation (sometimes called 'mimicry') but to an active, intentional form of imitation. This is certainly what the initial version of the AIM model proposed (Meltzoff & Moore, 1997).

There are at least two potential answers to this objection. First, although Meltzoff's earlier work made a firm distinction between automatic and intentional imitation, his more recent work suggests that this distinction may no longer be drawn and that AIM may now be understood to encompass automatic imitation. For example, in 2003 Meltzoff and Decety described the primary motor cortex, which is automatically activated when observing action (e.g. Fadiga et al., 1995), as a candidate neural substrate of imitation (p. 493).

Second, it can be argued that, whether or not it is recognised by Meltzoff, a theory of imitation which wishes to explain the correspondence problem is obliged to encompass automatic as well as intentional imitation. This is because both sets of phenomena pose the problem. For example, whether the sight of a model touching their ear (Chartrand & Bargh, 1999) makes me touch my ear automatically, or whether it does so via an intention to copy the model, it remains to be explained how my brain identifies the motor programme which will make my action look like that of the model from a third party perspective. There is no logical reason to implement two separate mechanisms which solve the same problem. In addition, there is some evidence that both intentional and automatic imitation rely on similar cortical areas, and therefore are likely to implement the same neurological mechanism in addition to the same psychological mechanism. That is, similar cortical areas are activated when observing and executing action and when intentionally imitating (Rumiati et al., 2005; Iacoboni et al., 1999), and no additional regions are activated in imitation tasks which are not activated in simple action observation or execution tasks.

If the ability to imitate is learned through associative learning, this would imply that mechanisms mediating imitation in adults are not present in neonates. Despite several studies providing support for the claim that neonates do imitate (Heimann, 1989; Heimann et al., 1989; Meltzoff & Moore, 1989; Kaitz et al., 1988; Reissland, 1988; Vinter, 1986; Kugiumutzakis, 1985; Field et al., 1983; Meltzoff & Moore, 1983; Field et al., 1982; Meltzoff & Moore, 1977), other studies have only found good evidence for neonatal imitation of tongue protrusion (Anisfeld et al., 2001; Ullstadius, 1998; Anisfeld, 1996; Anisfeld, 1991) and this may result from simple arousal (Jones, 1996; 2006). This suggests that the imitation which neonates are able to produce is mediated by innate reflexes which are replaced in later life by different mechanisms resulting in similar behaviour. This possibility is supported by the finding that any imitation which can be demonstrated with neonates, disappears at around three months of age (Heimann et al., 1989).

6.5 The role of experience in visuotactile integration

6.5.1 Summary and interpretation

Experiment 8 explored the role of experience and visual stimulus identity in visuotactile integration, assessing whether visuotactile integration can be modulated through training, and the dependency of any modulations on whether visual stimuli are human or non-human. Participants observed a rubber hand (View Hand group) or neutral object (View Object group) being stimulated synchronously or randomly with respect to their own unseen hand. Subsequent to these training phases, somatosensory ERPs were measured in response to tactile stimuli, and greater visuotactile integration was expected to be reflected by enhanced somatosensory processing of these tactile stimuli.

The results indicated that the N140 component of somatosensory processing is enhanced following synchronous stimulation of a hand or object stimulus and the participant's own hand, relative to uncorrelated stimulation conditions. This N140 modulation was independent of whether visual stimuli were human or non-human. These findings suggest that tactile processing in SII can be modulated by visuotactile associative learning. This pattern of results is inconsistent with any hypothesis which would suggest that visuotactile integration is mediated by innate mechanisms.

In addition, 200-450ms post-stimulus there was an enhanced negativity for stimuli presented to the hand which was compatible with the visual stimulus, compared with stimuli presented to the hand which was incompatible. This effect, which is thought to reflect an attentional bias towards the hand which received tactile stimulation during training, was present in every condition except the uncorrelated training condition in the View Hand group. This may be explained with reference to pre-existing body representations involving hand stimuli.

6.5.2 Limitations and outstanding questions

The influence of training on visuotactile integration in Experiment 8 has been interpreted as evidence of associative learning. An empiricist theory of a somewhat different nature is proposed by Armel & Ramachandran (2003) to account for modulations of visuotactile integration as a result of training, namely, Bayesian learning. Bayesian learning refers to a mathematical principle whereby the state of the world is estimated by combining sensory inputs which are weighted on the basis of the accuracy of each input. On the basis of statistical correlation between sensory inputs, Armel & Ramachandran (2003) propose that visual and tactile inputs become 'bound' (see also Ernst & Banks, 2002).

Armel & Ramachandran (2003) suggest that a Bayesian account of visuotactile integration can be contrasted with an associative learning account. They argue that an associative hypothesis would predict that delayed but correlated visuotactile inputs should result in visuotactile integration which is equal to that observed with synchronous inputs, but that their Bayesian model would predict greater integration with synchronous inputs. However, as already discussed in Chapter 1, associative learning is known to be sensitive, not only to contingency, but also to the temporal relationship between events (e.g. Mahoney & Ayres, 1976). Therefore, the results of previous experiments which find greater integration following synchronous stimulation conditions, relative to out-of-phase stimulation conditions, do not as Armel & Ramachandran (2003) suggest, favour a Bayesian account over an associative explanation; they are equally supportive of both. However, future theoretical work can further establish whether there are any necessary differences between Bayesian and associative learning, and, if so, what these may be.

The nature and origin of pre-existing body representations which may have led to observed differences in processing of human and non-human stimuli in Experiment 8 needs further investigation. If pre-existing body representations simply constitute pre-existing visuotactile links, then the results of Experiment 8 suggest that these are created through previous associative learning experiences with human stimuli. That is, as discussed in Chapter 1, those things which are modifiable are more likely to be learned than innate. To test the hypothesis that pre-existing visuotactile links could lead to a difference in processing of human and non-human stimuli, future research must establish that learning does not completely generalise between human and non-human stimuli.

However, if pre-existing body representations constitute something other than pre-existing visuotactile links, Experiment 8 cannot help elucidate the origin of these representations. The hypothesis that pre-existing body representations constitute something other than pre-existing visuotactile links is implied by Tsakiris & Haggard

(2005). The authors suggest that influences of stimulation type will only be observed if the visual stimulus fits with pre-existing body representations. If pre-existing body representations are simply pre-existing visuotactile links, then there is no reason to assume that these links with human stimuli can inhibit learning with non-human stimuli. The authors must therefore be implying that pre-existing body representations are something other than pre-existing visuotactile links with human stimuli, but they do not indicate specifically what these might be.

If the differences in processing of human and non-human stimuli observed in Experiment 8 reflect only previously learned associations between human visual stimuli and tactile stimuli, then human visuotactile integrative biases (greater integration with human stimuli, Thomas et al., 2006; Blakemore et al., 2005; Fiorio & Haggard, 2005; Press et al., 2004; Taylor-Clarke et al., 2004; Taylor-Clarke et al., 2002; Kennett et al., 2001; Graziano et al., 2000; Pavani et al., 2000) are likely to be modifiable through visuotactile training with non-human stimuli, in the same way as human imitative biases can be (Experiment 6). However, if pre-existing body representations which lead to differences in processing of human and non-human stimuli reflect something other than previously learned visuotactile associations with human stimuli, these modulations should not be observable. An experiment could assess this possibility in the following way. In a similar way to the test phases in Experiment 8, initial processing of tactile stimuli in somatosensory cortex could be assessed when simultaneously observing human or non-human stimuli. Subsequently, participants could be presented with either synchronous or uncorrelated visuotactile training with either human or non-human stimuli, and processing of tactile stimuli again assessed.

6.6 Conclusions

This thesis explored why human body movements are especially effective in eliciting imitative responses and what this suggests about the mechanisms mediating imitation. It was found that a human imitative bias is likely to be driven by perceptual properties of stimuli rather than knowledge about whether stimuli are or are not human. It was also found that imitation of non-human stimuli and the human imitative bias could be modulated through training. Stimuli with human perceptual properties may therefore elicit greater imitative responses than non-human stimuli because of greater opportunities for associative learning connecting human stimuli and matching responses. These findings are consistent with the Associative Sequence Learning model of imitation.

It was also found that training could modulate visuotactile integration; some modulations were independent of whether the visual stimulus was human or non-human, but other modulations showed dependence. Associative learning may therefore also explain integration of visual and tactile representations of events, but future research must establish why training can have different influences on visuotactile integration with human and non-human stimuli.

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