

How does visuomotor priming differ for biological and non-biological stimuli? A review of the evidence

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Abstract Visuomotor priming occurs when our actions are influenced by observing a compatible or incompatible action. Here we ask whether visuomotor priming is specific to human, biological actions or generalises to non-biological movements, such as abstract shapes or robots. Reviewing the evidence indicates that priming occurs for both types of stimuli and emphasises the contributions of both bottom-up (e.g. stimulus saliency, appearance, kinematics) and top-down (e.g. attention and prior knowledge) factors. We propose a model suggesting that although bottom-up features play a critical role, the degree of difference in priming for biological versus non-biological stimuli can be ultimately shaped by top-down factors.

The perception-action system

It is well known that there are intimate links between perception and action so that observation of an action can influence the observer's own motor system. For example, observing and performing a *compatible* action (e.g. lifting one's index finger while observing an index finger elevation) facilitates reaction times, whereas reaction times are slowed when observing a movement *incompatible* with a performed action (e.g. lifting one's index finger while

observing a finger press; Brass, Bekkering, & Prinz, 2001). These effects are collectively known as visuomotor priming or automatic imitation. One critical question is whether biological, human actions have a particularly strong perception-action linkage compared with non-biological movements, such as those produced by robots or abstract shapes. More specifically, is there something qualitatively different about biological actions (such as their kinematic structure) that enhances the perception-action linkage or are they just more attentionally salient?

It has been suggested that visuomotor priming may result from co-activation of compatible or incompatible sets of mirror neurons (Blakemore & Frith, 2005). Mirror neurons, originally identified in monkey ventral premotor cortex (human analogue, BA 44), discharge during both observation and execution of an action (Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neuroimaging of human participants suggests that functionally similar brain areas exist in homologous areas of premotor cortex and inferior parietal lobe (Buccino et al., 2001; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes, Armony, Rowe, & Passingham, 2003; Iacoboni et al., 1999; Rizzolatti et al., 1996). The speculative link between priming and mirror neurons is strengthened by the observation that priming is reduced following Transcranial Magnetic Stimulation (TMS) to an area of premotor cortex, the Inferior Frontal Gyrus (IFG; Catmur, Walsh, & Heyes, 2009). If priming is based on mirror neuron activation, then the perception-action system should respond preferentially to human actions. As will become apparent, however, visuomotor priming is not always unique to, or greater for, biological stimuli. This review will bring together work that has compared visuomotor priming for biological and non-biological stimuli to attempt to clarify whether priming differs between these two types of stimuli.

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Our review has been prompted by a number of recent developments. Firstly, there are concerns that apparent differences in priming between biological and non-biological stimuli may be accounted for by stimulus saliency. That is, biological stimuli may prime compatible actions simply because they are more salient (e.g. Jansson, Wilson, Williams, & Mon-Williams, 2007). Secondly, new work highlights the role of top-down factors such as attention and task instructions in visuomotor priming, suggesting that priming is not as automatic as initially thought (e.g. Longo, Kosobud, & Bertenthal, 2008). Thirdly, neuroimaging studies indicate that activity in brain areas that are part of the mirror neuron system is not confined to stimuli of biological origin (e.g. Gazzola, Rizzolatti, Wicker, & Keysers, 2007). In this review, we initially summarise those studies that have compared visuomotor priming in biological and non-biological stimuli (Table 1), then move on to highlight what factors influence the priming elicited by these stimuli. Finally, we provide a model that emphasises top-down modulation of priming and can explain many of the previous contradictory findings. The focus of this review is primarily on the behavioural effects of the two stimuli; see Press (2011) for discussion of behavioural and neural distinctions.

Measuring visuomotor priming

In a typical visuomotor priming paradigm, participants are presented with an action or movement on a screen. They must make a pre-specified response to either the onset of this movement or a separate go signal. Importantly, the characteristics of the observed action have no relevance to the participant's response. Compatibility, between this observed irrelevant action and the participant's response, is varied over trials. The degree of visuomotor priming is measured by the size of the compatibility effect; reaction times for compatible observation-execution pairs subtracted from incompatible couplings. This paradigm is based on the principles of Stimulus–Response compatibility (SRC: for a review see Heyes, 2011). SRC refers to the finding that similar stimuli and responses lead to faster reaction times due to stronger stimulus–response mappings (Cho & Proctor, 2003; Kornblum, Hasbroucq, & Osman, 1990; Vu & Proctor, 2004).

The basic priming task has been adapted in a number of ways, which can make comparing the results from different studies difficult. Firstly, paradigms can be divided into those that measure compatibility of the type of *movement* or the *effector* that is moved (Gowen, Bradshaw, Galpin, Lawrence, & Poliakoff, 2010; Heyes, 2011; although see Leighton & Heyes, 2010; Press, Gherri, Heyes, & Eimer, 2010 for rare examples whether the two paradigms have

been combined). For example, if one were making a press response with one's index finger, a movement compatibility effect would contrast viewing an index finger making a press response (compatible) with an index finger making a release response (incompatible). In contrast, an effector compatibility effect would contrast viewing an index finger (compatible) versus another finger (incompatible) making a press response (Fig. 1). Secondly, the participant may make a pre-planned response (as described above), that is they know that they will always be making a press response with their index finger or they may have a choice task, where their response is determined by the stimulus that they view. Interestingly, movement compatibility has nearly always been measured using a pre-planned task, while effector compatibility has always been measured using a choice task. Thirdly, the go signal may be the onset of the observed movement, the onset of a visual cue or an auditory tone. Fourthly, a range of different stimuli have been used including fingers, hands or arms for biological stimuli and robots or abstract shapes for non-biological stimuli. Fifthly, biological and non-biological stimuli are either presented within mixed or separate blocks. In the following paragraphs, we review the various studies comparing priming for biological and non-biological stimuli, summarised in Table 1. We consider how the above adaptations may have influenced the results. As movement and effector compatibility may call on different processes we review them separately (Vogt, Taylor, & Hopkins, 2003).

Movement compatibility

In one of the earliest studies on visuomotor priming, Stürmer, Aschersleben, and Prinz (2000) used movement direction to examine priming between a biological (human hand) and non-biological (bar) stimulus. Separate groups of participants observed either a video of a human hand spreading apart then closing, or a bar moving upwards or downwards. They had to make a predefined grasping or spreading action when the stimulus turned a particular colour. Priming was observed for both conditions, although the compatibility effects do appear smaller for the bar stimulus. Using a similar approach, Press, Bird, Flach, and Heyes (2005) used an opening or closing hand to elicit priming: actions were either compatible (observe hand opening, perform hand opening) or incompatible (observe hand opening, perform hand closing). They compared observation of a human and robot hand and found that although priming effects were greater for the human hand, significant priming effects were also present for the robot hand. Jansson, Wilson, Williams, and Mon-Williams (2007) repeated this study, but replaced the robot hand with two dots that could be close together or further apart. In contrast to the original findings, they observed equivalent priming for biological and non-biological stimuli.

Table 1 Overview of studies comparing biological with non-biological stimuli, divided according to whether movement or effector compatibility is measured (in chronological order)

Study	Priming	Stimuli	Blocked or mixed	Stimulus saliency	Spatial compatibility	Kinematics
<i>Movement Compatibility</i>						
Sturmer et al. (2000)	B > N	Human hand and bar (up/down movement)	Blocked	Uncontrolled	Uncontrolled	Unclear
Brass et al. (2001)	B only	Human finger (index) and black square (up/down movement)	Mixed	Uncontrolled	Uncontrolled	Controlled (B kinematics)
Kilner et al. (2003)	B only	Human arm and industrial robotic arm (horizontal/vertical movements)	Mixed	Uncontrolled	Uncontrolled	Uncontrolled
Press et al. (2005)	B > N	Human hand and robot (opening/closing)	Blocked	Semi-controlled (similar sizes)	Semi-controlled	Controlled (apparent movement)
Jansson et al. (2007)	B = N	Finger and pen (up/down movement)	Blocked	Controlled	Uncontrolled	Controlled (apparent movement)
Jansson et al. (2007)	B = N	Human hand and two dots (opening/closing)	Blocked	Uncontrolled	Semi-controlled	Controlled (apparent movement)
Poliakoff et al. (2007)	B > N	Human finger and square (up/down movement)	Mixed	Semi-controlled (separate go signal)	Uncontrolled	Controlled (B kinematics)
Gowen et al. (2010)	B only	Human finger and square (up/down movement)	Mixed	Semi-controlled (separate go signal)	Controlled	Controlled (B kinematics)
<i>Effector Compatibility</i>						
Brass et al. (2000)	B > N	Human index/middle finger (up/down movement) and Spatial X (appearance)	Blocked	Uncontrolled	Uncontrolled	Uncontrolled
Biermann-Rubens et al. (2008)	B > N ^a	Human index/middle fingers and red dots (up/down movement)	Mixed	Semi-controlled (separate go signal)	Uncontrolled	Controlled (B kinematics)

The table also details whether the stimuli were mixed or presented in separate blocks and whether stimulus saliency, spatial compatibility and kinematics were controlled for the two stimulus types (columns 4–7)

B biological, N non-biological

^a Unclear from results whether a significant difference between compatible and incompatible trials exists for each type of stimulus (only interaction presented)

In a similar manner, Brass et al. (2001) compared the effects of upward/downward biological (moving index finger) or non-biological motion (a moving black square). In one block, participants were instructed to make a finger press and in the other block a finger lift. In compatible trials, stimulus and action were in the same direction, whereas in incompatible trials they were in different directions (e.g. observed finger lift, executed finger press). Significant compatibility effects were observed for the finger movement only, with a non-significant trend for the moving object. However, Jansson et al. (2007) repeated the Brass et al. (2001) study, but presented biological and non-biological stimuli in separate blocks, and found visuospatial priming effects in both cases. Poliakoff, Galpin, Dick, Moore, and Tipper (2007) and Gowen et al. (2010) used a similar paradigm to Brass et al. (2001), but asked participants to respond to the onset of an “X” go signal, following

the observation of a moving finger or square. Poliakoff and colleagues found that priming was greater for the biological stimulus in a group of elderly participants, whereas Gowen et al. (2010) observed significant priming for the biological stimulus only in a group of younger adults.

Using a different approach, Kilner, Paulignan, and Blakemore (2003) measured spatial interference effects as opposed to reaction times. The participant moved their arm in time with that of an actor. Compatible movements are those in the same plane (e.g. both vertical), while incompatible movements are in different planes (e.g. actor moves in horizontal plane, participant in vertical plane). Movements made while observing an incompatible action show greater variation in the plane of the incompatible movement, termed movement interference. Kilner et al. observed that movement interference was present for the human actor, but not an industrial robotic arm.

Effector compatibility

Brass, Bekkering, Wohlschläger, and Prinz (2000) compared priming between a moving finger and a spatial cue. In each trial, either the index or middle finger lifted and an “X” appeared on the fingernail of one of the fingers. In the *spatial cue* block, participants chose whether to lift their index or middle finger according to which finger the “X” appeared on, while in the *finger movement condition*, participants were required to lift the finger according to which finger they observed move. Brass and colleagues hypothesised that as the moving finger matches the response more closely than the spatial cue, reaction times should be faster when responding to the moving finger, which they found to be the case. Compatibility effects were examined for the task-irrelevant aspect of the stimulus; the location of the spatial cue when attending to the moving finger and the moving finger when attending to the location of the spatial cue. They found that an incompatible finger movement had a larger influence on spatial cue trials, compared to the effect of the spatial cue on finger movement trials, suggesting a stronger influence of a biological movement. However, as this paradigm measures the degree to which reaction times are influenced by concurrent stimuli appearing in different locations, it may measure the capture of exogenous attention by different stimuli, rather than direct priming of the visuomotor system (see Chong, Cunnington, Williams, & Mattingley, 2009 for a similar view). Therefore, this methodology is not ideal to examine differences in priming between biological and non-biological stimuli.

Biermann-Ruben et al. (2008) used a modified version of an effector compatibility choice task in which participants lifted either their index or little finger depending on which tone they heard. In the biological condition, prior to the tone, they observed a series of irrelevant lifting and depressing finger movements of either the index or little finger, while in the non-biological condition, the finger movements were replaced with a red dot movement up and down over either finger. The tone occurred either at the onset or at offset of the final finger/dot movement. As the final observed movement was always downwards and the participant’s action was always a finger lift, both the onset and offset conditions are additionally influenced by the type of movement, that is there are actually two compatibility components (effector and movement). Consequently, the results are difficult to interpret and we just focus on the onset findings, when movement direction is compatible. Reaction times were faster in the compatible (effector) conditions for both stimuli, but there was significantly more priming for the biological condition.

In summary, while the majority of studies show that priming is greater for, or restricted to, observation of a biological stimulus, two studies found no difference in priming between the two types of stimuli. In the next section, we explore possible factors that influence the level of priming for either type of stimuli.

Factors influencing priming

Stimulus saliency

One potential confound is that stimulus saliency may differ, with non-biological stimuli tending to be smaller, covering less surface area and dimmer than the biological stimuli. From Table 1, column 5 it can be seen that the majority of studies do not control for stimulus saliency, meaning that the smaller compatibility effects for the non-biological stimulus may merely reflect them being less noticeable and less attention-grabbing. Effector compatibility tasks and those that use the onset of the observed movement as the go signal are particularly susceptible to stimulus saliency confounds, since greater relevance is placed on detecting the observed movement. Aicken, Wilson, Williams, and Mon-Williams (2007) tackled this issue directly by increasing the size of the X in the task used by Brass et al. (2000). They observed that reaction times were now actually faster when responding to the X and there was no influence of the moving finger when responding to the X. Saliency effects have also been reported in movement compatibility experiments; when Jansson et al. (2007) modified the study by Brass et al. (2001), where a trend for compatibility effects in the non-biological stimulus was observed, they found similar levels of priming for a finger stimulus and a more visually salient pen movement. Although their stimuli were unmatched for angular displacement, this work highlights that, at the very least, experimenters should attempt to equate the stimulus characteristics for the two stimulus types. It may indicate, however, as argued by Jansson and colleagues (2007), that apparent differences in priming between biological and non-biological stimuli are only due to saliency, with such differences only occurring when stimulus saliency is unequal. Nevertheless, as will be discussed in the next section, it appears that stimulus saliency confounds cannot completely account for all reported findings. For example, when we attempted to reduce stimulus saliency confounds by using the same go signal for biological and non-biological stimuli, we still observed greater priming for the biological stimulus (Gowen et al., 2010; Poliakoff et al., 2007). However, although the go signal was the same in both conditions, the stimuli themselves still differed in size and brightness.

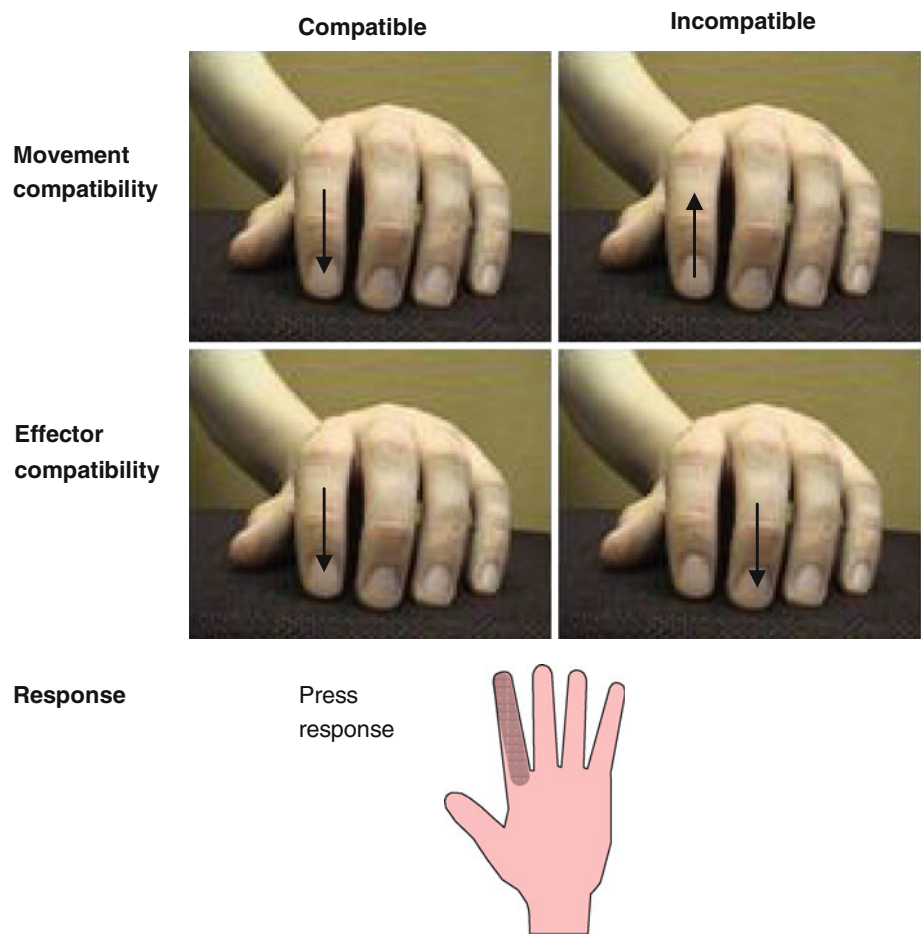
Stimulus response compatibility

Another consideration is the possibility that priming represents SRC effects that are not specific to imitation of biological actions. Spatial SRC effects occur where responses are faster to spatially aligned stimuli (Cho & Proctor, 2003). For example, in an effector compatibility task, if the participant views a mirror image of the right hand that they are using to respond, a moving index finger on the left also maps onto the spatial location of the participants own index finger (Fig. 1), i.e. it has *lateral spatial compatibility*. Therefore, one should remove as many of these non-specific SRC effects and examine what level of priming is left for the relevant dimension. Some studies have attempted this by removing spatial SRC effects and support the presence of an “imitative component” separate to spatial compatibility (Bertenthal, Longo, & Kosobud, 2006; Catmur and Heyes, 2011). Heyes (2011) has extensively reviewed this area and suggests that compatibility effects attributed to priming can be separated from spatial SRC. For example, Catmur and Heyes (2011) used an effector compatibility choice task where participants responded to a colour cue with abduction of either their

index or little finger. Critically, the hand stimulus that they observed could be either a right or left hand so that all different combinations of spatial compatibility (the observed finger and response finger on the same side) and effector compatibility (the observed finger and response finger anatomically the same) could be tested. Both effector and spatial compatibility contributed separate components to the overall compatibility effect and exhibited different time courses with spatial compatibility occurring earlier.

The same kind of approach has also been used in a movement compatibility task (up/down movement); Brass et al. (2001) horizontally flipped the observed hand so that the direction of the finger movement did not match the response, e.g. an upward finger movement was seen to move downward, whilst still priming an upward finger movement. This enabled them to measure an effect of movement compatibility for a moving finger that was independent of the observed direction. Lateral spatial compatibility (left–right position of the stimulus) is of less importance in movement compatibility tasks compared to effector choice tasks, since it cannot confound the compatibility effect of interest and because there is less visual

Fig. 1 An illustration of the different types of compatibility effect, measured for a press response with the index finger. A *movement compatibility* effect compares viewing the index finger making a press movement (compatible) and the index finger making a release movement (incompatible). An *effector compatibility* effect compares viewing the index finger making a press movement (compatible) and the middle finger making a press movement (incompatible)



processing of the stimulus for a pre-planned response (Vogt et al. 2003). Nevertheless, it may still exert an influence¹. However, Gowen et al. (2010) showed that the up/down priming from a finger was greater than that of a moving block, whether the observed moving finger was on the same side (viewing a mirror image left hand) or on the opposite side (viewing a right hand) as the right hand index finger they used to respond.

Although the above studies indicate a priming component specific to biological stimuli, they do not rule out the possibility that this component is based on the principles of SRC. While Specialist theories of imitation argue that imitation of human actions is mediated by a dedicated and unique imitation mechanism, Generalist theories argue that imitation depends on more general motor processes (see Brass & Heyes, 2005 for a review). One generalist theory is the associative sequence learning (ASL) model (Cook, Press, Dickinson, & Heyes, 2010; Heyes, 2001, 2010), which is based on the associative stimulus–response mechanisms involved in Pavlovian and instrumental conditioning. It is proposed that there are a series of excitatory links between sensory and motor aspects of the same action that form from experience of self-observation and being imitated. The ASL model suggests that greater visuomotor priming may occur for human stimuli due to more experience of observing and executing human actions leading to correlated visuomotor associations. Supporting this possibility, Press, Gillmeister, and Heyes (2007) showed that priming produced by a robotic hand reached similar levels to that of a human hand following compatible training with the robot hand. Therefore, smaller priming effects for non-biological stimuli may simply be due to less experience of these stimuli leading to weaker stimulus–response associations.

Quite clearly, the evidence indicates that both experience and visual saliency play a role in the level of priming for biological and non-biological stimuli. However, it is far from clear how these factors interact and the following observations suggest that other factors may also be at play. Firstly, the effect of correlated visuomotor experience reported by Press et al. (2007) argues against a fixed role for stimulus saliency, as we would not expect priming to increase when saliency remains the same. In addition, it is unclear why Jansson et al. (2007) found equivalent priming for a hand and two dots which were clearly unmatched in terms of stimulus saliency, whereas Press et al. (2005) found less priming for a robot compared to human hand, which arguably differed less in saliency. Similarly, whereas Kilner et al. (2003) found no movement

interference for a robot arm, Jansson et al. (2007) observed interference when participants observed a moving dot: if SRC and saliency factors were key to producing interference it is unclear as to why none was found for the large and obvious industrial robotic arm. On the other hand, if visuomotor experience is the key factor in determining priming, why did Jansson et al. (2007) observe equivalent priming for pens, moving dots and fingers? In addition to these points, there are a number of findings relating to stimulus kinematics and top-down control that are difficult to explain using either experience or saliency and are discussed in the following sections.

Movement kinematics

Biological and non-biological stimuli have different movement kinematics: human movements contain more variability and have a non-linear profile, whereas non-biological stimuli move with a constant velocity profile (Hogan, 1984). To what extent is priming to biological compared to non-biological affected by either the kinematics or appearance of stimuli? In studies that have controlled for both stimulus saliency and kinematics, by giving the two stimulus types the same biological motion, one would expect priming to be equal if kinematics were the key. However, it can be seen from Table 1, that priming is solely confined to, or greater for the biological stimulus in a number of such studies suggesting that appearance is more influential. On the other hand, some studies suggest that kinematics do affect priming (see Press, 2011). Kilner, Hamilton, and Blakemore (2007) compared movement interference when participants watched either a ball or human arm moving with a biological or non-biological velocity profile. When observing the human arm movement, interference was only apparent with biological kinematics, but interference was present for both movement profiles when observing the ball stimulus. Bouquet, Gaurier, Shipley, Toussaint, and Blandin (2007) also reported similar interference for both biological and non-biological kinematics, when participants observed a moving dot. These results suggest a complex interaction between kinematics and appearance for human stimuli: the unusual combination of non-biological kinematics and human form removed interference. Furthermore, interference has only been found for biological compared to artificial kinematics when using a humanoid robot (Chaminade, Franklin, Oztop, & Cheng, 2005; Oztop, Franklin, Chaminade, & Cheng, 2005). Therefore, priming for biological stimuli does appear to be influenced by both kinematics and appearance, whereas there is less impact of biological kinematics when stimuli appear artificial. It is difficult to understand these results using just visual saliency or experience.

¹ We did, however, observe an effect of view on the size of compatibility effects in a condition which required people to attend closely to the movement of the finger or block and report odd-ball movements. This manipulation also removed the difference between biological and non-biological stimuli.

Top-down factors

There is increasing evidence that top-down processes related to social cognition can influence lower level perceptual and motor processes (Teufel, Fletcher and Davis, 2010). For example, paying close attention during action observation has been found to increase sensorimotor responses (Muthukumaraswamy & Singh, 2008). In regards to automatic imitation, as highlighted by Heyes (2011), the same stimuli can elicit different levels of priming according to top-down factors such as instructions and attention. In a movement interference task, we asked participants to move their arm in time with a moving dot either in the compatible or incompatible direction (Stanley, Gowen, & Miall, 2007). The dot moved with kinematics that matched a human actor (biological) or with an artificial constant velocity (non-biological). We compared movement interference in two groups of participants: one group was instructed that both dots were computer generated, and the other group was instructed that both dots were pre-recorded human arm movements. Thus, the relative importance of movement kinematics and the “belief” that the movements were of human origin could be contrasted. Interestingly, interference was only observed in the group who had been given the human agency instructions across both the biological and non-biological conditions. Therefore, in addition to movement kinematics and appearance, interference is strongly influenced by prior knowledge regarding the agency of the movement. Longo and Bertenthal (2009) and Liepelt and Brass (2010) also observed that priming for moving fingers was reduced when participants were explicitly told or shown that the same hand was virtual or wooden as opposed to real (see Tsai & Brass, 2007 for a related finding). There does however, appear to be a limit to this top-down influence. Press, Gillmeister, and Heyes (2006, Exp. 2) compared the effect of instruction on a schematic picture of a hand with biological movement and a schematic, angular robot hand that moved in a non-biological manner. Questionnaire data suggested that instructions significantly altered belief for the two stimuli, with participants judging the stimuli presented under “human” instruction as more animate. Although priming was smaller for the robotic stimuli, the amount of priming was unaffected by the instruction for either stimulus. Here, it seems that even if people believe stimuli to be of a particular origin, these top-down effects have less weighting when bottom-up information relating to appearance and kinematics is unambiguous.

It is worth considering whether the choice of stimuli in different studies may have implicitly led to beliefs or affective states being formed which influenced whether differences in priming between biological and non-biological stimuli were observed. A well-known phenomenon

in the field of robotics is the uncanny valley. As one gradually makes a robot (or virtual character) more human-like in its appearance and kinematics, one might predict a linear increase in how much the robot is liked. There is however, an “uncanny valley of eeriness”, whereby people experience a strong aversion to characters that are close to, but fall short of, being human (Mori, 1970). This response has been widely documented in humans and an analogous response has recently been observed in monkeys (Steckenfinger & Ghazanfar, 2009). Such a response in a particular experiment may have led to a reduction in priming by what was meant to be a biological stimulus or a non-biological stimulus. In the latter case, a stimulus that is more human-like (e.g. a robot hand), with a particular combination of kinematics and appearance, could in fact produce less priming than a more abstract non-biological stimulus that does not generate this emotional response. Possible routes by which priming might be modulated by this emotional aversion are discussed in the next section.

Finally, we have also observed that priming from the same stimuli can be influenced by attentional state (Gowen et al., 2010). Using a similar paradigm to Poliakoff et al. (2007), participants watched an upward or downward moving index finger or square and made a predefined key press or lift when a “X” cue appeared on the finger at the end of the movement (Experiment 1). Compatibility effects were only present for the biological finger condition. However, when the X cue was replaced by a diffuse flash, priming was observed for both types of stimulus (Experiment 2a), suggesting that when attention was less focussed on the moving finger or square, stimulus differences were not reflected in the level of priming. These results indicate that differentiation of the two stimulus types may be an active process. A further observation, that may be explained by attention, is that when trials of biological and non-biological stimuli are mixed within the same block of trials (Brass et al., 2001; Gowen et al., 2010; Kilner et al., 2003), priming for non-biological stimuli is more likely to be non-significant (Table 1). In contrast, when presented as separate blocks, priming is significant for non-biological stimuli (Brass et al., 2000; Jansson et al., 2007; Press et al., 2005; Stürmer et al., 2000). We suggest that under the mixed block context, attention is drawn to the differences between the stimuli, leading to a modulation in priming.

Modelling visuomotor priming

The review so far indicates that any account of visuomotor priming needs to take account of the effects of stimulus saliency and experience, as well as the different priming responses that occur when kinematic profiles or attention and instructions vary. In this section, we introduce a model

that attempts to integrate these findings in order to explain priming for non-biological and biological stimuli. We make a distinction between pure biological stimuli where the kinematics and appearance are human, non-biological stimuli, which are entirely abstract and have no previous association with human movements and ambiguous stimuli, which are artificial in nature, but share characteristics with human appearance or kinematics (e.g. robotic or wooden hands, abstract shapes with biological kinematics).

The model comprises two main routes (Fig. 2). The visuomotor route consists of parietal and frontal circuits involving the translation of visual information into action via SRC mechanisms which produces visuomotor priming by facilitating or interfering with the programming of the participant's response. In line with previous suggestions, priming along this route could occur via two mechanisms (Chong, Williams, Cunnington, & Mattingley, 2008; Hamilton, 2008; Rizzolatti, Fadiga, Fogassi, & Gallese, 2002; van Schie et al., 2008). One mechanism is a relatively low-level form of priming which occurs in an automatic manner and is dependent on bottom-up factors such as visual saliency and experience with the stimuli. The other mechanism is a higher level, taking into account action goals. Both biological (black arrows) and non-

biological (striped arrows) are processed within the visuomotor pathway, although they are likely to involve different neural areas (Casile et al., 2010). For example, only signals from biological stimuli would be processed by the superior temporal sulcus (STS), which is consistently involved in biological motion (Bonda, Petrides, Ostry, & Evans, 1996; Grossman, Battelli, & Pascual-Leone, 2005). The visuomotor route is similar to the direct route of Ferrari, Bonini, and Fogassi (2009) and the long-term SRC associations described by Heyes (2011), although our definition is broader to take into account movement goals and the processing of both biological and non-biological stimuli.

Our model also comprises a modulating, top-down route involving areas within the prefrontal cortex that receive and process information relating to appearance, kinematics, prior instructions, context and attention. This route may modulate priming via the inferior frontal gyrus, which has been associated with inhibition of visuomotor priming (Bien, Roebroek, Goebel, & Sack, 2009; Brass, Derrfuss, & von Cramon, 2005; Chong et al., 2008; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005). For non-biological stimuli, if attention is drawn to the non-biological nature of the stimulus, priming may be inhibited. The other main

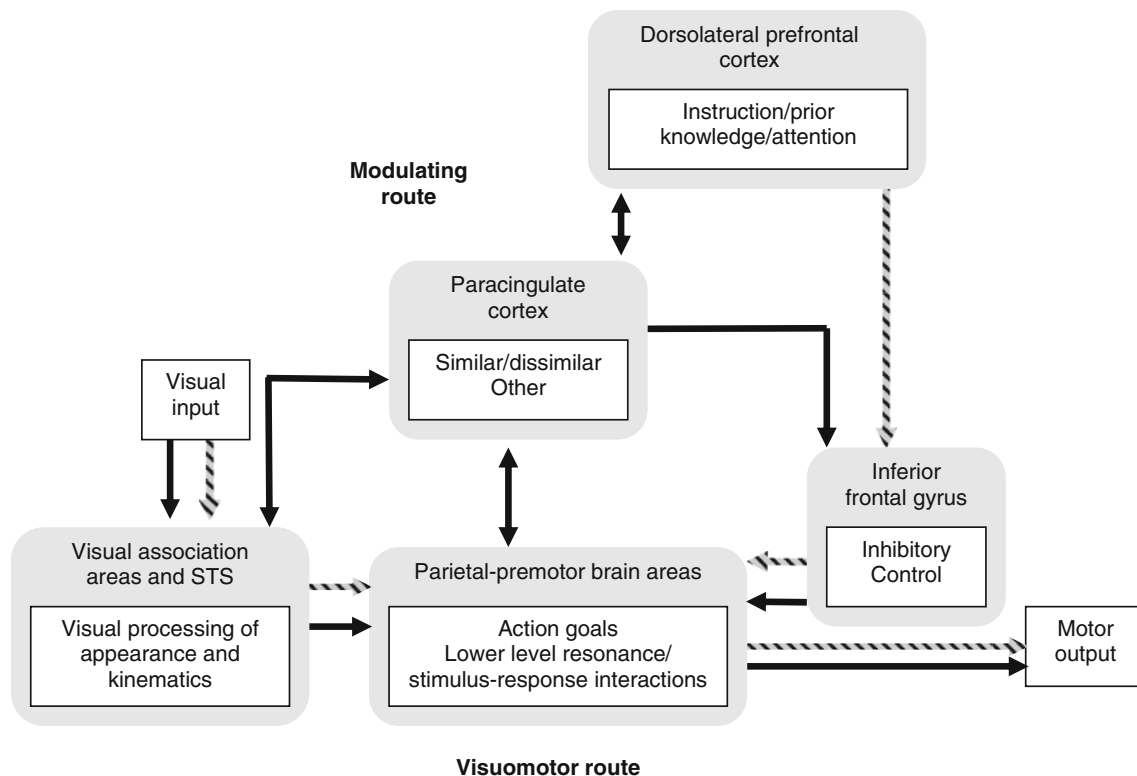


Fig. 2 Visual information relating to stimuli deemed to be biological (black lines) and non-biological (striped lines) is transformed into motor output to produce priming along the visuomotor route. This route is influenced by the modulating pathway consisting of prefrontal areas. When observing human-related stimuli, information regarding

appearance, kinematics and prior knowledge is integrated within this route to weight how similar the stimulus is to oneself. If the stimulus is dissimilar, priming is inhibited via the IFG. In the case of non-biological stimuli, if attention is directed towards the nature of the stimulus, priming would be inhibited via the IFG

area involved in the modulating route is an area within the medial prefrontal cortex (mPFC), the paracingulate cortex, which is thought to play a role in tasks that require the predicting and understanding of human actions and characteristics, as well as those involving self referential processing (Amodio & Frith, 2006; Castelli, Happe, Frith, & Frith, 2000; Frith & Frith, 2006; Gallagher et al., 2000; Gallagher & Frith, 2003; Krach et al., 2008; Mitchell, Banaji, & Macrae, 2005a, 2005b; Mitchell, Heatherton, & Macrae, 2002; Ramnani & Miall, 2004). In line with work suggesting a dissociation between actions and more complex processes relating to social understanding (Van Overwalle & Baetens, 2009), we suggest that in the context of action observation, this area only becomes active when conflicting signals within the visuomotor route arise or top-down factors suggest that the origin of the stimulus (human versus non-biological) is important. Under such circumstances, we propose that the paracingulate cortex forms a type of “comparator” where signals regarding kinematics, appearance and prior knowledge are analysed to interpret the stimulus. This integration of top-down and bottom-up signals shares similarities with the predictive coding account (Kilner, Friston, & Frith, 2007) and a recent model by Chaminade and Cheng (2009), where input about the stimulus properties is compared to our predictions in order to gauge how closely the stimulus meets our expectations. However, in our model, the paracingulate cortex provides a possible integration site where these various predictions and prediction errors meet and are assimilated.

This comparator role of the paracingulate cortex is supported by evidence that the paracingulate cortex is divided into at least two different functional regions: ventral and dorsal (Jenkins, Macrae, & Mitchell, 2008; Mitchell et al., 2005b; Mitchell, Macrae, & Banaji, 2006). In a recent study (Stanley, Gowen, & Miall, 2010), we examined brain activity while we manipulated participants’ beliefs about whether an observed stimulus was of a human or computer origin. We found that the ventral paracingulate cortex was mainly responsive to the human instruction, whereas the dorsal region of the paracingulate cortex was active when the stimulus and instructions were inconsistent. Thus, the ventral paracingulate may encode stimuli deemed to be similar to ourselves, whereas dorsal paracingulate cortex may process information from ambiguous scenarios where prior knowledge or appearance and stimulus content are not easily reconciled. Supporting this idea, Marsh and Hamilton (2011) reported that paracingulate activity differentiated between observed rational and irrational actions. Therefore, we suggest that the paracingulate cortex becomes active when conflict arises or further analysis of the stimulus is required: if the stimulus is judged as a dissimilar other, the dorsal paracingulate will be activated and priming along the visuomotor route will

be inhibited. Inhibition could arise either through feedback to the STS (Teufel, Fletcher, & Davis, 2010), via direct connections from the paracingulate cortex to the visuomotor route or via the IFG. Equally, if the observer has prior knowledge that the stimulus is human-generated or similar to themselves, the ventral paracingulate cortex may become active and enhance priming via the aforementioned connections. This relationship between the paracingulate cortex and motor areas remain speculative at present, as no activation was observed in premotor areas or the IFG during the human instruction condition in our previous study (Stanley et al., 2010). However, a link between the paracingulate cortex and visuomotor priming is supported by recent evidence showing that tasks relating to ToM, self-referential processing and imitation activate similar areas of the mPFC (Spengler, von Cramon, & Brass, 2009) and that ToM ability and level of priming is correlated (Spengler, von Cramon, & Brass, 2010).

At present, there is insufficient evidence to understand exactly how the visuomotor or modulating route of our model processes the various forms of ambiguous stimuli. In a related model, Chaminade and Cheng (2009) have suggested that the strength with which a stimulus activates bottom-up processes depends on whether there are existing representations of the action: this would be strongest for human stimuli, intermediate for humanoid robots and nonexistent for industrial robots. When top-down processes occur to interpret the bottom-up input from the humanoid robot, this would produce a large predictive error signal as predictions regarding what a human stimulus should look like are violated by the humanoid form. This predictive error would become smaller, the more closely the humanoid robot resembled a human. Therefore, the manner in which ambiguous stimuli are processed is likely to depend on a combination of stimulus properties as well as prior knowledge and attention. For example, Carter, Hodgins, and Rakison (2011) compared brain activity during observation of grasping actions by either a human actor, a humanoid robot with biological kinematics, a robot constructed out of abstract blocks with biological kinematics or a mechanical claw with artificial kinematics. They found that STS activity increased when the human actor and humanoid robot shifted or missed the goal, but no modulation was apparent for the other two stimuli. In addition, mPFC activity was greater for the former two stimuli. These findings suggest that the actions of the human actor and humanoid robot were processed similarly and activated the modulatory route when goals and kinematics were mismatched. In contrast, the block robot and claw were not processed in terms of goals and perhaps just activated neural circuits within the visuomotor route.

According to our model, visuomotor priming for both biological, non-biological and ambiguous stimuli can be

influenced in three ways. Firstly, if bottom-up factors relating to stimulus appearance and kinematics of a biological stimulus are in conflict this may be detected by the STS and forwarded to the paracingulate cortex, which modulates the level of priming. An example would be the observation that movement interference for a human or humanoid arm only occurs if the kinematics are human rather than artificial (Chaminade et al., 2005; Kilner, Hamilton, et al., 2007; Oztop et al., 2005). Indeed, a humanoid arm may be processed in a similar way to a human arm, as highlighted by similar brain activity following observation of the actions of a humanoid robot and human actor (Carter et al., 2011). Mismatch between appearance and kinematics has been directly examined in an fMRI paradigm measuring brain responses during observation of (1) a human (2) a humanoid robot moving with non-biological kinematics and (3) the same robot as in (2) moving with identical non-biological kinematics, but with the human features stripped off, leaving metal (Saygin, Chaminade, Ishiguro, Driver, & Frith, 2011). Greater repetition suppression was observed in parietal areas for the humanoid robot compared to the other two conditions, suggesting higher neural activity for the humanoid robot. Saygin et al. (2011) interpret these findings according to predictive coding framework, where brain activity is highest when predictions are violated, with a large error produced by the mismatch between the human appearance and non-biological kinematics. Referring back to our earlier discussion of the “uncanny valley of eeriness”, such a mismatch may lead to both modulation of priming and the sense that the stimulus is in some way eerie.

Secondly, priming can be modulated if the appearance and/or kinematics of the action are inconsistent with any action goals. The goal of an action may be higher or lower level: lower level goals can refer to grasping an object along with its associated sub-goals (move arm, open fingers, etc.), while higher-level goals can refer to communicative actions. Liepelt, Prinz, and Brass (2010) demonstrated that priming in response to a wooden hand only occurred when the action appeared appropriate to the wooden hand. For example, priming occurred to grasping an apple, but not to a communicative gesture. Here it seems, that a wooden hand grasping an object is not unexpected, possibly due to our exposure to animals and robots lifting and moving objects. One important aspect of this experiment was that participants responded 1,915 ms after presentation of the stimulus, providing enough time for higher level processing of the meaning of the action and possible activation of the modulating route. Integration of the different visual and contextual signals within the paracingulate cortex may have led to top-down control over priming via the IFG. If participants had been asked to respond immediately following stimulus presentation,

priming may also have been present for the communicative gesture.

Thirdly, top-down factors such as prior instructions and attention may modulate priming. In the case of instructions highlighting the non-biological nature of a stimulus, inhibition of priming may occur via the DLPFC-IFG route. This is consistent with studies showing that priming to identical human-like stimuli is reduced when participants are led to believe the stimuli are artificial (Liepelt & Brass, 2010; Longo & Bertenthal, 2009). It is important to note that priming in these previous studies was reduced, but not eliminated by the non-biological belief condition indicating that instructions or prior knowledge are less effective when stimulus appearance is unambiguous. Indeed, instructions do not affect priming when appearance and kinematics are matching as in the case of a human-like hand moving biological kinematics (Press et al., 2006). Under such circumstances, where stimulus properties and instructions are in conflict, our model suggests that the paracingulate cortex compares these conflicting bottom-up and top-down inputs and modulates the degree of priming according to how related the stimulus is to oneself. In cases where stimulus appearance may be more ambiguous, as with a moving dot (Stanley et al., 2010), there may be less conflict between the stimulus and knowledge, so instruction has more weighting: we observed interference for the human instruction, but no interference for the computer instruction. Alternatively, Press (2011) suggests that greater attention to the dot in the human belief condition could have produced greater priming for the “human” compared to “computer” instruction condition. Although this is a possibility that requires further exploration, we think that it is unlikely to explain the results of Stanley et al. since interference for moving dot stimuli is consistently observed in experiments that do not involve instruction conditions (Bouquet et al., 2007; Jansson et al., 2007; Kilner, Friston, et al., 2007; Kilner, Hamilton, et al., 2007; Stanley et al., 2007, Experiment 1). It is therefore surprising that no interference was observed for the moving dot in the “computer” instruction condition. Consequently, we suggest that our belief manipulation inhibited interference for the “computer” instruction and maintained a baseline level of interference for the “human” instruction. In order to confirm this, we would need to compare interference between an instruction and no instruction condition. Interestingly, it has recently been observed that prior priming of social concepts led to an increase in the compatibility effect from moving fingers both in a movement compatibility (Leighton, Bird, Orsini, & Heyes, 2010) and an effector compatibility task (Cook and Bird, 2011). This suggests that responses to biological stimuli can be boosted under the right circumstances, although there was no non-biological baseline in these experiments. It remains to be

seen whether a negative mood induction, or emotional aversion (such as the “uncanny valley”) reduce priming. A further question is whether this integration of top-down and bottom-up signals occurs each time the stimulus is presented (i.e. on each trial) or whether integration occurs early in the experiment and leads to a “baseline” inhibition or enhancement of priming throughout the experiment.

The influence of attention in our model can explain why priming for highly unnatural non-biological stimuli occurs in some studies but is absent in others. As mentioned earlier, priming in these cases appears to be related to the context in which the stimuli are presented—priming for non-biological stimuli is usually absent in the mixed trial context, but present when using separate blocks. When presented in isolated blocks, we suggest that priming relies on the visuomotor route with no top-down influence. The strength of priming is dependent on bottom-up aspects such as stimulus saliency and experience. This can explain interference during observation of a ball for both biological and non-biological kinematics (Bouquet et al., 2007; Jansson et al., 2007; Kilner, Friston, et al., 2007; Kilner, Hamilton, et al., 2007)². However, in the mixed trial presentation mode, we suggest that attention is drawn to the differences between the stimuli, so that priming for the non-biological stimulus is inhibited via the DLPFC-IFG route. Our previous results regarding attention would fit with the idea that differentiating the two stimuli is an active process (Gowen et al., 2010); when attention is more diffuse, less importance is placed on differentiating the stimulus form and priming occurs unmodulated along the visuomotor route. Similarly, priming for biologically implausible movements is only apparent until the participant’s attention is drawn to the impossible nature of movements (Longo et al., 2008). Therefore, attention is likely to play an important role in the regulation of priming, shaping the degree to which kinematics, appearance and goals interact along the visuomotor route.

Summary and conclusions

Our review examining visuomotor priming for biological and non-biological stimuli indicates that priming can occur for both stimulus types. We have proposed a model where all types of stimuli are processed along a visuomotor route where priming is dependent on factors relating to stimulus saliency, experience and SRC. Priming to non-biological is dependent on attention: if attention is drawn to the non-biological characteristics of the stimulus, priming may be

inhibited via the DLPFC and IFG. Priming to biological stimuli (and some ambiguous forms) depends on the integration of stimulus properties such as appearance, kinematics, goals or prior knowledge within the paracingulate cortex, which modulates the degree of priming according to how similar the observed stimulus is to oneself. Therefore, the degree of priming for biological compared to non-biological stimuli is determined by an inter-dependent communication between bottom-up and top-down factors.

Returning to our original question, it appears that biological stimuli are “special” in that providing cognitive resources and attention are available, our brains may be tuned to compare the kinematics, appearance, goals and context of stimuli in order to assess whether they are similar to ourselves and whether they conform to our predictions. Our model fits with the idea that social cognition should be viewed as an interplay between higher cognitive processes and lower level perceptual and motor responses (Spengler et al., 2010; Teufel et al., 2010) and the notion that action understanding requires both the mirror neuron system and higher Theory of Mind areas (Brass, Schmitt, Spengler, & Gergely, 2007; Csibra, 2007; Kilner and Frith, 2008; Uddin, Iacoboni, Lange, & Keenan, 2007). The distinction between similar/dissimilar other in the paracingulate cortex could bridge the gap between motor and social processes. Our model shares similarities with a recent model proposed by Heyes (2011) where long-term SRC associations (similar to our visuomotor route) are modulated by input (attention related) and output (social cognitive) factors. However, we have attempted to provide a more detailed description of how kinematics may be integrated with top-down factors and have specifically focussed the comparison between biological and non-biological stimuli. In addition, input factors in our model would include stimulus saliency, SRC and kinematics, whereas attention could modulate priming at both the input and output stage.

A number of aspects within the model remain unclear at present. One of these is which types of stimuli are analysed by the STS and paracingulate cortex. At the extremes, one can assume that human stimuli are analysed by the STS, whereas entirely artificial stimuli are processed by different visual areas. However, the situation is less clear for ambiguous stimuli. This becomes more complicated when you add a prior belief condition. Similarly, it remains unclear how these different stimuli are processed along the visuomotor route. As mentioned earlier, while overlap is emphasised by recent evidence that mirror system areas are active during observation of actions by non-biological stimuli (Cross, Hamilton, Kraemer, Kelley, & Grafton, 2009; Engel, Burke, Fiehler, Bien, & Rosler, 2008; Gazzola et al., 2007; Oberman, McCleery, Ramachandran, & Pineda, 2007), the extent of this overlap may be

² Here we have suggested that the movement of a single dot with or without biological kinematics are processed similarly but this requires further clarification.

dependent on how closely these stimuli relate to the observer's actions. For example, the non-biological action may have been physically experienced (Cross et al., 2009) or associated with familiar object goals (Gazzola et al., 2007). In such a case, one would expect that non-biological stimuli presented without any biological context should activate different areas within the visuomotor route.

Finally, our model could have implications for unconscious social mimicry and the 'uncanny valley'. Recent evidence suggests that the degree to which we engage in social mimicry is modulated by factors such as how focussed our attention is on those around us and how affiliated we feel to people (Stel et al., 2010; Van Baaren et al., 2009). The integration of kinematic, appearance and context related signals within the modulating route may modulate the degree of social mimicry and our feelings of affiliation or 'eeriness', thus determining both the degree of priming and our emotional response to a stimulus, with the paracingulate cortex being a key area.

References

- Aicken, M. D., Wilson, A. D., Williams, J. H., & Mon-Williams, M. (2007). Methodological issues in measures of imitative reaction times. *Brain and Cognition*, *63*, 304–308.
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Review Neuroscience*, *7*, 268–277.
- Bertenthal, B. I., Longo, M. R., & Kosobud, A. (2006). Imitative response tendencies following observation of intransitive actions. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 210–225.
- Bien, N., Roebroek, A., Goebel, R., & Sack, A. T. (2009). The brain's intention to imitate: the neurobiology of intentional versus automatic imitation. *Cerebral Cortex*, *19*, 2338–2351.
- Biermann-Ruben, K., Jonas, M., Kessler, K., Siebner, H. R., Baumer, T., Schnitzler, A., et al. (2008). Observing repetitive finger movements modulates response times of auditorily cued finger movements. *Brain and Cognition*, *68*, 107–113.
- Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, *43*, 260–267.
- Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human-parietal systems, and the amygdala, in the perception of biological motion. *The Journal of Neuroscience*, *16*, 3737–3744.
- Bouquet, C. A., Gaurier, V., Shipley, T., Toussaint, L., & Blandin, Y. (2007). Influence of the perception of biological or non-biological motion on movement execution. *Journal of Sports Science*, *25*, 519–530.
- Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica (Amst)*, *106*, 3–22.
- Brass, M., Bekkering, H., Wohlschlagler, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, *44*, 124–143.
- Brass, M., Derrfuss, J., & von Cramon, D. Y. (2005). The inhibition of imitative and overlearned responses: a functional double dissociation. *Neuropsychologia*, *43*, 89–98.
- Brass, M., & Heyes, C. (2005). Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Science*, *9*(10), 489–495.
- Brass, M., Schmitt, R. M., Spengler, S., & Gergely, G. (2007). Investigating action understanding: inferential processes versus action simulation. *Current Biology*, *17*, 2117–2121.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Carter, E. J., Hodgins, J. K., & Rakison, D. H. (2011). Exploring the neural correlates of goal-directed action and intention understanding. *Neuroimage*, *54*, 1634–1642.
- Casile, A., Dayan, E., Caggiano, V., Hendlar, T., Flash, T., & Giese, M. A. (2010). Neuronal encoding of human kinematic invariants during action observation. *Cerebral Cortex*, *20*, 1647–1655.
- Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage*, *12*, 314–325.
- Catmur, C., & Heyes, C. (2011). Time course analyses confirm independence of imitative and spatial compatibility. *Journal of Experimental Psychology: Human Perception and Performance*, *37*, 409–421.
- Catmur, C., Walsh, V., & Heyes, C. (2009). Associative sequence learning: The role of experience in the development of imitation and the mirror system. *Philosophical Transactions of the Royal Society London B: Biology Science*, *364*, 2369–2380.
- Chaminade, T., & Cheng, G. (2009). Social cognitive neuroscience and humanoid robotics. *Journal of Physiology-Paris*, *103*(3–5), 286–295.
- Chaminade, T., Franklin, D., Oztop, E., and Cheng, G. (2005). Motor interference between humans and humanoid robots: effect of biological and artificial motion. In *Proceedings of the 4th International Conference on Development and Learning**, Osaka, Japan.
- Cho, Y. S., & Proctor, R. W. (2003). Stimulus and response representations underlying orthogonal stimulus-response compatibility effects. *Psychonomic Bulletin and Review*, *10*, 45–73.
- Chong, T. T., Cunnington, R., Williams, M. A., & Mattingley, J. B. (2009). The role of selective attention in matching observed and executed actions. *Neuropsychologia*, *47*, 786–795.
- Chong, T. T., Williams, M. A., Cunnington, R., & Mattingley, J. B. (2008). Selective attention modulates inferior frontal gyrus activity during action observation. *Neuroimage*, *40*, 298–307.
- Cook, J., & Bird, G. (2011). Social attitudes differentially modulate imitation in adolescents and adults. *Experimental Brain Research*, *211*, 601–612.
- Cook, R., Press, C., Dickinson, A., & Heyes, C. (2010). Acquisition of automatic imitation is sensitive to sensorimotor contingency. *Journal of Experimental Psychology: Human Perception and Performance*, *36*, 840–852.
- Cross, E. S., Hamilton, A. F., Kraemer, D. J., Kelley, W. M., & Grafton, S. T. (2009). Dissociable substrates for body motion and physical experience in the human action observation network. *European Journal of Neuroscience*, *30*, 1383–1392.
- Csibra, G. (2007). Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rosetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition. Attention and performance XXII* (pp. 435–459). Oxford: Oxford University Press.
- Engel, A., Burke, M., Fiehler, K., Bien, S., & Rosler, F. (2008). How moving objects become animated: the human mirror neuron system assimilates non-biological movement patterns. *The Society for Neuroscience*, *3*, 368–387.
- Ferrari, P. F., Bonini, L., & Fogassi, L. (2009). From monkey mirror neurons to primate behaviours: possible 'direct' and 'indirect'

- pathways. *Philosophical Transactions of the Royal Society London B: Biology Science*, 364, 2311–2323.
- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, 50, 531–534.
- Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of ‘theory of mind’. *Trends in Cognitive Science*, 7, 77–83.
- Gallagher, H. L., Happe, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: an fMRI study of ‘theory of mind’ in verbal and nonverbal tasks. *Neuropsychologia*, 38, 11–21.
- Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *Neuroimage*, 35, 1674–1684.
- Gowen, E., Bradshaw, C., Galpin, A., Lawrence, A., & Poliakoff, E. (2010). Exploring visuomotor priming following biological and non-biological stimuli. *Brain and Cognition*, 74, 288–297.
- Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Experimental Brain Research*, 112, 103–111.
- Grezes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to “mirror” and “canonical” neurones in the human brain: an fMRI study. *Neuroimage*, 18, 928–937.
- Grossman, E. D., Battelli, L., & Pascual-Leone, A. (2005). Repetitive TMS over posterior STS disrupts perception of biological motion. *Vision Research*, 45, 2847–2853.
- Hamilton, A. F. (2008). Emulation and mimicry for social interaction: a theoretical approach to imitation in autism. *Quarterly Journal of Experimental Psychology*, 61(1), 101–115.
- Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Science*, 5, 253–261.
- Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience and Biobehavioral Reviews*, 34(4), 575–583.
- Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, 137, 463–483.
- Hogan, N. (1984). An organizing principle for a class of voluntary movements. *Journal of Neuroscience*, 4, 2745–2754.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286(5449), 2526.
- Jansson, E., Wilson, A. D., Williams, J. H., & Mon-Williams, M. (2007). Methodological problems undermine tests of the ideomotor conjecture. *Experimental Brain Research*, 182, 549–558.
- Jenkins, A. C., Macrae, C. N., & Mitchell, J. P. (2008). Repetition suppression of ventromedial prefrontal activity during judgments of self and others. *Proceedings of the National Academy of Sciences of United States of America*, 105, 4507–4512.
- Kilner, J. M., & Frith, C. D. (2008). Action observation: Inferring intentions without mirror neurons. *Current Biology*, 18, R32–R33.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cognitive Processing*, 8(3), 159–166.
- Kilner, J., Hamilton, A. F., & Blakemore, S. J. (2007). Interference effect of observed human movement on action is due to velocity profile of biological motion. *The Society for Neuroscience*, 2, 158–166.
- Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Current Biology*, 13, 522–525.
- Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitive basis for stimulus-response compatibility—a model and taxonomy. *Psychological Review*, 97, 253–270.
- Krach, S., Hegel, F., Wrede, B., Sagerer, G., Binkofski, F., & Kircher, T. (2008). Can machines think? Interaction and perspective taking with robots investigated via fMRI. *PLoS ONE*, 3(7), e2597.
- Leighton, J., Bird, G., Orsini, C., & Heyes, C. M. (2010). Social attitudes modulate automatic imitation. *Journal of Experimental Social Psychology*, 46, 905–910.
- Leighton, J., & Heyes, C. (2010). Hand to mouth: Automatic imitation across effector systems. *Journal of Experimental Psychology: Human Perception and Performance*, 36(5), 1174–1183.
- Liepelt, R., & Brass, M. (2010). Top-down modulation of motor priming by belief about animacy. *Experimental Psychology*, 57, 221–227.
- Liepelt, R., Prinz, W., & Brass, M. (2010). When do we simulate non-human agents? Dissociating communicative and non-communicative actions. *Cognition*, 115, 426–434.
- Longo, M. R., & Bertenthal, B. I. (2009). Attention modulates the specificity of automatic imitation to human actors. *Experimental Brain Research*, 192, 739–744.
- Longo, M. R., Kosobud, A., & Bertenthal, B. I. (2008). Automatic imitation of biomechanically possible and impossible actions: effects of priming movements versus goals. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 489–501.
- Marsh, L. E., & Hamilton, A. F. (2011). Dissociation of mirroring and mentalising systems in autism. *Neuroimage*, 56, 1511–1519.
- Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005a). General and specific contributions of the medial prefrontal cortex to knowledge about mental states. *Neuroimage*, 28, 757–762.
- Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005b). The link between social cognition and self-referential thought in the medial prefrontal cortex. *Journal of Cognitive Neuroscience*, 17, 1306–1315.
- Mitchell, J. P., Heatherton, T. F., & Macrae, C. N. (2002). Distinct neural systems subserve person and object knowledge. *Proceedings of the National Academy of Sciences of United States of America*, 99, 15238–15243.
- Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron*, 50, 655–663.
- Molnar-Szakacs, I., Iacoboni, M., Koski, L., & Mazziotta, J. C. (2005). Functional segregation within pars opercularis of the inferior frontal gyrus: evidence from fMRI studies of imitation and action observation. *Cerebral Cortex*, 15, 986–994.
- Mori, M. (1970). The uncanny valley. *Energy*, 7, 33–35. (in Japanese).
- Muthukumaraswamy, S. D., & Singh, K. D. (2008). Modulation of the human mirror neuron system during cognitive activity. *Psychophysiology*, 45, 896–905.
- Oberman, L. M., McCleery, J. P., Ramachandran, V. S., & Pineda, J. A. (2007). EEG evidence for mirror neuron activity during the observation of human and robot actions: toward an analysis of the human qualities of interactive robots. *Neurocomputing*, 70, 2194–2203.
- Oztop, E., Frankline, D. W., Chaminade, T., & Cheng, G. (2005). Human–humanoid interaction: is a humanoid robot perceived as a human? *International Journal of Humanoid Robotics*, 2, 537–559.
- Poliakoff, E., Galpin, A., Dick, J., Moore, P., & Tipper, S. P. (2007). The effect of viewing graspable objects and actions in Parkinson’s disease. *Neuroreport*, 18, 483–487.
- Press, C. (2011). Action observation and robotic agents: learning and anthropomorphism. *Neuroscience and Biobehavioral Reviews*, 35(6), 1410–1418.
- Press, C., Bird, G., Flach, R., & Heyes, C. (2005). Robotic movement elicits automatic imitation. *Brain Research Cognitive Brain Research*, 25, 632–640.
- Press, C., Gherri, E., Heyes, C., & Eimer, M. (2010). Action preparation helps and hinders the perception of action. *Journal of Cognitive Neuroscience*, 22(10), 2198–2211.

- Press, C., Gillmeister, H., & Heyes, C. (2006). Bottom-up, not top-down, modulation of imitation by human and robotic models. *European Journal of Neuroscience*, *24*(8), 2415–2419.
- Press, C., Gillmeister, H., & Heyes, C. (2007). Sensorimotor experience enhances automatic imitation of robotic action. *Proceedings: Biological Science*, *274*(1652), 2509–2514.
- Ramnani, N., & Miall, R. C. (2004). A system in the human brain for predicting the actions of others. *Nature Neuroscience*, *7*, 85–90.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (2002). From mirror neurons to imitation: facts and speculations. In A. N. Meltzoff & W. Prinz (Eds.), *The imitative mind*. Cambridge, UK: Cambridge University Press.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research Cognitive Brain Research*, *3*, 131–141.
- Saygin, A. P., Chaminade, T., Ishiguro, H., Driver, J., Frith, C (2011) The thing that should not be: Predictive coding and the uncanny valley in perceiving human and humanoid robot actions. *Social Cognitive and Affective Neuroscience* (in press).
- Spengler, S., von Cramon, D. Y., & Brass, M. (2009). Control of shared representations relies on key processes involved in mental state attribution. *Human Brain Mapping*, *30*, 3704–3718.
- Spengler, S., von Cramon, D. Y., & Brass, M. (2010). Resisting motor mimicry: control of imitation involves processes central to social cognition in patients with frontal and temporo-parietal lesions. *The Society for Neuroscience*, *5*, 401–416.
- Stanley, J., Gowen, E., & Miall, R. C. (2007). Effects of agency on movement interference during observation of a moving dot stimulus. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 915–926.
- Stanley, J., Gowen, E., & Miall, R. C. (2010). How instructions modify perception: an fMRI study investigating brain areas involved in attributing human agency. *Neuroimage*, *52*, 389–400.
- Steckenfinger, S. A., & Ghazanfar, A. A. (2009). Monkey visual behavior falls into the uncanny valley. *Proceedings of the National Academy of Sciences of United States of America*, *106*, 18362–18366.
- Stel, M., van Baaren, R. B., Blascovich, J., van, D. E., McCall, C., Pollmann, M. M., van Leeuwen, M. L., Mastop, J. & Vonk, R. (2010) Effects of a priori liking on the elicitation of mimicry. *Experimental Psychology* *57*, 412–418
- Sturmer, B., Aschersleben, G., & Prinz, W. (2000). Correspondence effects with manual gestures and postures: a study of imitation. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 1746–1759.
- Teufel, C., Fletcher, P. C., & Davis, G. (2010). Seeing other minds: attributed mental states influence perception. *Trends in Cognitive Science*, *14*, 376–382.
- Tsai, C. C., & Brass, M. (2007). Does the human motor system simulate Pinocchio's actions? Coacting with a human hand versus a wooden hand in a dyadic interaction. *Psychological Science*, *18*, 1058–1062.
- Uddin, L. Q., Iacoboni, M., Lange, C., & Keenan, J. P. (2007). The self and social cognition: the role of cortical midline structures and mirror neurons. *Trends in Cognitive Science*, *11*, 153–157.
- van Baaren, R., Janssen, L., Chartrand, T. L., & Dijksterhuis, A. (2009). Where is the love? The social aspects of mimicry. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 2381–2389.
- Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage*, *48*, 564–584.
- van Schie, H. T., Koelewijn, T., Jensen, O., Oostenveld, R., Maris, E., & Bekkering, H. (2008). Evidence for fast, low-level motor resonance to action observation: an MEG study. *The Society for Neuroscience*, *3*, 213–228.
- Vogt, S., Taylor, P., & Hopkins, B. (2003). Visuomotor priming by pictures of hand postures: perspective matters. *Neuropsychologia*, *41*, 941–951.
- Vu, K. P., & Proctor, R. W. (2004). Mixing compatible and incompatible mappings: elimination, reduction, and enhancement of spatial compatibility effects. *Quarterly Journal of Experimental Psychology A*, *57*, 539–556.