Biological tuning of mirror mechanisms: Evidence and functional implications

Clare Press

Department of Psychological Sciences, Birkbeck, University of London

Tel: +44 (0) 20 3073 8007

Email: c.press@bbk.ac.uk

Word count, excluding references: 5767

Figures: Two greyscale

Boxes: Two

ABSTRACT

A range of behavioural and neuroimaging evidence demonstrates that we mirror observed human action in our motor systems to a greater extent than similar non-biological movement. This chapter reviews such evidence, considering the form and kinematic features of observed stimuli to which mirror mechanisms are sensitive. It subsequently considers the role of this biological tuning in our interactions with, and processing of, humans relative to inanimate devices, in the context of functions likely to be supported by mirror mechanisms. It notes that in contrast with common assumptions, biological tuning is unlikely to reflect increased inferential processing about mental states of observed humans. It considers that biological tuning is more likely to influence our imitation and perception of human and inanimate movements. The final section examines how biological tuning can be integrated with evidence that mirror mechanisms are part of a wider domain-general system adapted for action control, mapping motor codes onto observed events from both our social and inanimate environments.

1 Introduction

Observation of action activates the motor codes required for performance. For example, we automatically imitate others when there is no intention to have done so and no reported awareness of matching behaviour (e.g. Chartrand and Bargh, 1999). Consistent with these behavioural data, neuroimaging studies demonstrate that observing action activates an 'action observation network' (AON), including motor structures such as ventral and dorsal premotor cortices, posterior regions of the inferior frontal gyrus and primary motor cortex (Rizzolatti and Craighero, 2004). In homologous areas 'mirror neurons' have been found in the macaque, that discharge not only when the monkey executes an action of a certain type (e.g. precision grip), but also when it observes the experimenter or another monkey performing that action (Cisek and Kalaska, 2004; Dushanova and Donoghue, 2010; Gallese et al., 1996; Pellegrino et al., 1992). Furthermore, neuroimaging adaptation techniques demonstrate that populations of cells with mirror properties are likely to exist in these areas in humans (Kilner et al., 2009; Lingnau et al., 2009; Press et al., 2012a, 2012b). Motor mirror mechanisms (hereafter, simply mirror mechanisms) have been proposed to support a wide range of social and non-social functions, from intention reading (Iacoboni et al., 2005) through to aesthetic experience (Di Dio and Gallese, 2009).

Concurring with some of these hypothesized functions, studies investigating the properties of mirror mechanisms typically demonstrate biological tuning, such that human actions activate corresponding motor codes to a greater extent than non-biological movements. This chapter will begin by reviewing behavioural and neuroimaging studies that demonstrate biological tuning, considering the form and kinematic features of observed stimuli to which mirror mechanisms are sensitive. It will define mirror mechanisms functionally – that they support

the activation of corresponding, or mirroring, motor codes during action observation. According to this definition, the cardinal features of mirror mechanisms are (1) that a motor code is activated during action observation, and (2) that it is the code required for performing *that specific* action. Both behavioural and neuroimaging studies can demonstrate that motor codes are activated during action observation, but behavioural methods are often superior for demonstrating specificity. For example, the classic studies conducted by Chartrand and Bargh (1999) demonstrate that observation of a confederate scratching their head elicits head scratching, rather than foot shaking behaviour, and observation of foot shaking elicits foot shaking. In contrast, neuroimaging studies rarely provide evidence of specificity, often simply demonstrating that motor structures are active when observing action (unless employing adaptation or multivariate pattern classification techniques; Oosterhof et al., 2013). Despite these limitations, neuroimaging studies will be reviewed in the present chapter given that they largely concur with the behavioural data. Functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies demonstrating observation-related activation in motor circuits will be outlined, alongside magnetocephalography (MEG) studies examining attenuation of central beta (15-30 Hz) oscillations. Alpha (7-14 Hz) oscillatory studies will not be included, due to recent evidence that these effects relate to tactile, rather than motor, mirroring (Coll et al., submitted). This section will conclude that there is evidence for tuning both with respect to the form and kinematic profile of observed movements.

The chapter will subsequently consider the role of biological tuning in our interactions with, and processing of, humans relative to inanimate devices, in the context of functions likely to be supported by mirror mechanisms. First, it will establish that there is little evidence for a role of mirror mechanisms in inferential sociocognitive functions required to support a theory of mind, and therefore that in contrast with common assumptions, biological tuning is unlikely to

reflect inferential processing about mental states of humans, but not inanimate entities. Second, it will outline preliminary evidence that mirror mechanisms support various types of imitation and action perception, and consider how biological tuning may influence our imitation and perception of human and inanimate movements. Third, it will examine how biological tuning can be integrated with the view that mirror mechanisms are part of a wider domain-general system adapted for action control, thereby mapping motor codes to observed events from both our social and inanimate environments.

2 Evidence of biological tuning

2.1 Behavioural evidence

Kilner et al. (2003) showed that the execution of sinusoidal arm movements in a vertical or horizontal plane was subject to interference from simultaneous observation of another human performing arm movements in the opposite plane; if participants executed vertical arm movements while observing horizontal movements, there was greater variance in the horizontal dimension, compared with conditions where they observed vertical movements (Fig. 1a). This 'interference effect' is thought to be a result of the automatic activation of motor codes which correspond to observed action, and an interaction between these motor codes and those required for executing the intended action. When the observed movements were made by a robotic arm, there was no interference effect. However, there were at least two differences between the human and non-human stimuli presented in this experiment. First, the stimuli differed in form. Namely, the human stimuli were a flesh colour, rounded, and had a certain joint configuration, whereas the non-biological stimuli were more geometric and with fewer joints. Second, the stimuli differed in kinematics. The human arms followed an approximately minimum jerk trajectory, where the movement is slow at turning points and faster on straight

trajectories (Hogan, 1984), whereas the robotic stimulus moved with constant velocity. A number of studies have controlled for one of these factors while measuring the effect of the other, to investigate whether one or both of form and kinematics generate the biological tuning within mirror mechanisms (see Box 1 for related studies that investigate the top-down influence of belief about stimulus identity on biological mirror mechanism activation).

In a simple reaction time (RT) task, Brass et al. (2001) found evidence of greater activation of corresponding motor codes when stimuli had a human, rather than point, form, and were matched for kinematics. Participants were required to make a pre-specified index finger lifting or tapping movement whenever they saw the index finger of an observed hand move. They were faster to execute this movement (e.g. finger lifting) in response to observed compatible (lifting) rather than incompatible (tapping) movements. This effect has been termed the 'automatic imitation' effect, given that it signifies primed imitative, relative to non-imitative, responses (see Fig. 1b), and for similar reasons to the interference effect, is considered to reflect automatic activation of motor codes which correspond to observed actions (NB. Automatic imitation and interference effects are not thought to be differentially dependent upon priming versus inhibition, respectively – both effects are likely driven by both processes - but the common nomenclature is used in this chapter to differentiate the paradigms). Brass and colleagues (2001) found no evidence of an automatic imitation effect when responses were made to a point that moved up or down with the same kinematic profile as the observed finger actions. Gowen et al. (2010) replicated this finding of a form x compatibility interaction when comparing automatic imitation of index / middle finger lifting movements relative to similar movement of geometric shapes. Likewise, in a paradigm akin to that employed by Kilner et al. (2003), Gowen et al. (2008) found a greater interference effect when participants

observed a real human model performing movements which were incongruent with their own, relative to a point on a computer monitor moving with a similar kinematic profile.

Influences of form on motor activation have also been found when the non-human stimuli are structurally more similar to the human stimuli. Press et al. (2005) investigated differences in processing of human and robotic form, while controlling for kinematics, by removing kinematic information and simply presenting end state postures of movement. Using a simple RT procedure, they required participants to execute a pre-specified hand opening or closing response whenever an observed stimulus hand in a neutral posture was replaced by a hand in an open (fingers splayed) or closed (fist) posture. Participants were faster to execute the action (e.g. hand opening) in response to observed compatible (open) rather than incompatible (closed) postures. This automatic imitation effect was larger when observing human hands than robotic hands (Fig. 2a; see also Bird et al., 2007; Press et al., 2007, 2006 for the same effect). Similarly, Cook et al. (2014) found greater interference effects when participants observed human avatar form stimuli compared with robotic form stimuli. These studies therefore indicate that stimuli with human form activate corresponding motor codes to a greater degree than stimuli with closely matched non-biological form. Interestingly, Kupferberg et al. (2012) found that interference effects with a robotic arm were similar to those with a human arm if the joint configurations matched those of a human arm (Fig. 2b). Similarly, there was no evidence of greater automatic imitation of finger movements made by an avatar hand rather than inanimate blocks with the same 'joints' (Klapper et al., 2014). Therefore, form effects may be determined solely by configural joint features, not other stimulus properties such as skin tone, concurring also with the finding that biological tuning remains when all stimuli are presented in the same – inanimate – tone (Press et al., 2005).

Other behavioural studies have examined the effects of kinematics on processing in mirror mechanisms. These studies have indicated that, when stimuli are matched for form, movements with human kinematics sometimes generate greater motor activation than movements with non-biological kinematics. For example, Chaminade et al. (2005) found larger interference effects when a humanoid robot form stimulus moved with human kinematics rather than an artificially generated trajectory, and Kilner et al. (2007) found more interference when participants observed human form stimuli that moved with human kinematics rather than constant velocity. However, the same effect was not found by Kilner et al. (2007) when watching a point move with the two kinematic profiles, and both Gowen et al. (2008) and Cook et al. (2014) failed to find evidence that the kinematic profile influenced the magnitude of an interference effect. Therefore, kinematic manipulations sometimes generate a biological bias, although these effects are not detected in all studies.

2.2 Neuroimaging evidence

A number of imaging studies support these behavioural findings. For example, a PET study found that the observation of human grasping actions activates premotor cortex to a greater degree than the observation of similar robotic actions (Tai et al., 2004). Additionally, in three fMRI studies, stronger premotor and pIFG activation was found when participants observed meaningless human hand movements relative to the movements of yellow objects (Engel et al., 2008; BA6), human finger actions relative to scissor movements (Costantini et al., 2005; BA44), and humans rather than robots dancing (Miura et al., 2010; BA44 and BA6).

Neuroimaging studies have also demonstrated influence of either form or kinematics, while controlling for the other stimulus variable. For example, Saygin et al. (2004) found that

observing human motion represented by points of light attached to each joint resulted in greater premotor activation than when points with the same kinematic trajectories were scrambled such that a human form was no longer implied. Additionally, a virtual reality near-infrared spectroscopy study found evidence of biological tuning according to kinematic features; demonstrating greater sensorimotor activation when a human form model grasped objects with human, rather than constant velocity, kinematics (Shimada, 2010 N.B. There was not the same effect of kinematics in a robotic form condition). An MEG study reached a similar conclusion: Press et al. (2011) presented participants with human form or point form vertical sinusoidal arm actions, which moved with human or constant velocity kinematics. When observing movements with human kinematics, beta oscillations changed across time in a manner that would be expected if executing the actions. No such dynamic modulations were seen when observing movements with constant velocity kinematic profiles. These dynamic modulations were observed regardless of whether the stimulus had a human or point form.

Effects of kinematics have also been demonstrated when the non-biological kinematic profile is matched to the human profile for complexity. One PET study (Stevens et al., 2000) showed greater primary motor cortex activation when participants observed an arm movement video that was played at a rate that made it biologically plausible, compared with when it was played more rapidly. Two fMRI studies have similarly indicated that, both when stimuli are of point (Dayan et al., 2007; BA6 and BA44) and human (Casile et al., 2010; dorsal BA6) form, observing movements obeying the two-thirds power law (Lacquaniti et al., 1983) - that slow down at curved relative to straight parts of motion, which broadly speaking corresponds to a minimum jerk trajectory - activates premotor and pIFG structures to a greater extent than observing movements with the inverted kinematic profile. These studies therefore indicate that stimuli

with human kinematics consistently activate motor areas to a greater extent than stimuli with non-biological kinematics when the two profiles are matched for complexity.

One fMRI study observed equal motor activation when observing human and constant velocity robotic grasping actions (Gazzola et al., 2007; although if applying a $p < 0.001$ uncorrected threshold, some of the human actions generated greater activation than some of the robotic actions at BA6 coordinates). Additionally, Gobbini et al. (2011) found similar premotor activation when observing human and humanoid emotional facial expressions (in fact, there was a larger response for humanoid actions at some coordinates). Given that the humanoid robot in this study was matched so closely in form to the human stimuli, including joint configurations, these findings concur with those of Kupferberg et al. (2012) – that human joint configurations are the important form feature that determines mirror activation. Similarly, Cross et al. (2012) found that when the joint configurations of a Lego figure were matched to those of human whole body stimuli (see Fig. 2c), typical biological tuning effects were not obtained.

Therefore, most neuroimaging studies support the behavioural data by demonstrating greater motor activation when observing human relative to non-biological movement, in structures such as the dorsal and ventral premotor cortex, and posterior regions of the IFG. As non-biological stimuli become more human-like, for example, by exhibiting human joint configurations, biological tuning effects disappear. Therefore, despite the poorer demonstration of specificity in these studies, the evidence concurs with the behavioural data.

2.3 Biological tuning evidence: Conclusion

In summary, there have been a number of studies indicating greater operation of mirror mechanisms when observing human action, relative to similar non-biological movement. There are observable influences both of the form and the kinematics of the stimuli.

3 Functional implications of biological tuning

It has long been hypothesised that mirror mechanisms allow us to 'understand' others' actions 'from within' (Gallese and Sinigaglia, 2011; Rizzolatti et al., 1996). Under this hypothesis, biological tuning reflects greater 'understanding' of humans compared to inanimate devices. Indeed it has been suggested that when mirror mechanisms are active during the observation of non-human agents like humanoid robots, it is a sign of ascription of human properties such as mental states to these agents (e.g. Chaminade and Cheng, 2009; Gazzola et al., 2007; Oberman et al., 2007). For example, Oberman et al. (2007) claim 'the implication is that the human mirror neuron system may be activated as a result of the human interactant anthropomorphising these robots. Indeed, by activating the human mirror neuron system humanoid robots could potentially tap into the powerful social motivation system inherent in human life, which could lead to more enjoyable and longer lasting human-robot interactions' (p.2195). Similarly, Gazzola et al. (2007) say 'now we know, that our mirror neuron system may be part of the reason why, when in Stars Wars, C3PO taps R2D2 on the head in a moment of mortal danger, we cannot help but attribute them human feelings and intentions, even if their physical aspect and kinematics are far from human' (p.1683). Furthermore, Chaminade

and Cheng (2009) state 'the underlying assumption is that the measure of …(motor activation) indicates the extent to which an artificial agent is considered as a social inter-actor' (p. 289).

The term 'action understanding' was introduced by Rizzolatti and colleagues to characterize the function of mirror neurons (Rizzolatti and Fadiga, 1998; Rizzolatti et al., 1996). However, there is still no consensus about exactly what is meant by 'action understanding', and how it differs from inferential mentalising, perceptual or motoric functions (Gallese et al., 2011). Therefore, the following section will first consider the potential role of mirror mechanisms in distinct, operationally established, functions involved in understanding and interacting with others. These functions are mentalising, imitation and action perception. In each case it will consider what biological tuning can tell us about processing of humans and inanimate devices. Second, it will examine how biological tuning can be integrated with the view that mirror mechanisms are part of a wider domain-general system adapted for action control, thereby mapping motor codes onto observed events from both our social and inanimate environments.

3.1 Mentalising, imitation and action perception

Initial investigations have suggested that mirror mechanisms are unlikely to be involved in inferential processes required for intention understanding. For example, Brass et al. (2007) found no changes in motor activation when manipulating the difficulty of intention inference associated with observed actions. Similarly, de Lange et al. (2008) found that requiring participants to attend to the intention underlying an action did not increase activation in motor circuits relative to attention to the means by which an action was executed. Instead, these manipulations generated differences in other regions such as the medial prefrontal cortex, which have been classically associated with social inferential functions. Therefore, claims that

operation of mirror mechanisms – when observing either human or inanimate models – reflects the extent to which we 'attribute them human feelings and intentions' (Gazzola et al., 2007) are premature, if not inaccurate.

There is better evidence that mirror mechanisms are involved in imitation, and therefore that biological tuning influences the nature of imitated events. Automatic imitation is considered a demonstration of the operation of mirror mechanisms (defined functionally as in the present chapter, rather than anatomically – remember that this functional definition relies solely upon demonstration that action observation activates motor codes for performing that action). Therefore, by definition, mirror mechanisms are involved in such imitation. There are known positive effects of automatic imitation, for example, interactions are perceived as smoother, and interactees are rated more positively (Chartrand and Bargh, 1999), and humans may typically benefit from these effects to a greater extent than their inanimate counterparts such as robots. For these reasons, stimulus variables are often tuned to equate automatic imitation of humanoid robots with that of humans to enhance the 'social competence' of robots (Marin et al., 2009). There is also evidence that we rely upon the same mechanisms during intentional imitation. For example, damage to the inferior frontal cortex results in impaired imitation of finger movements (Goldenberg and Karnath, 2006), and transcranial magnetic stimulation (TMS) studies have demonstrated that stimulation of premotor / pIFG regions disrupts both intentional and automatic imitation of simple finger and hand actions (Catmur et al., 2009; Heiser et al., 2003; Newman-Norlund et al., 2010). Therefore, biological tuning of mirror mechanisms likely contributes to greater intentional imitation of humans than inanimate devices. Intentional imitation is likely to facilitate acquisition of skills and behaviours (Heyes, 1993), and therefore we will be able to learn a number of skills from conspecifics in a way that we do not with inanimate devices.

Finally, a handful of studies have considered whether activation of mirror representations aids perception of action. Patient and TMS studies suggest that a top-down contribution of mirror mechanisms to perception is likely, given that lesions to motor regions can impair perception (see R. Cook et al., 2014 for a review). Therefore, the motor system may contribute to perception of human actions to a greater extent than that of inanimate movement. Some initial investigations support this possibility. For example, Candidi et al. (2008) demonstrated that TMS of pIFG (BA44) impaired the ability of participants to discriminate two kinematically possible arm and leg actions, but had no effect on their performance in distinguishing two kinematically impossible movements.

In summary, biological tuning within mirror mechanisms may have at least two functional implications. First, we will likely imitate humans more than inanimate devices. Therefore, we will be able to learn a number of skills from conspecifics in a way that we do not with inanimate devices, and humans may benefit from the effects of automatic imitation to a greater extent. Second, the motor system may contribute to perception of human actions more than non-human movements. However, biological tuning is less likely to reflect processing about mental states of an observed entity because there is no evidence that mirror mechanisms are involved in such processing.

3.2 Biological tuning within a domain-general perception-action mapping mechanism

There is emerging evidence that mirror mechanisms are not genetic adaptations specifically for mirroring the actions of others, but rather, emerge through domain-general processes of sensorimotor associative learning within a system adapted for action control (see Catmur,

present volume). It may seem counterintuitive that biological tuning is seen within such a system that is not specifically designed for social functions. However, in fact biological tuning is predicted under this account given that we have had more correlated experience of observing human action - rather than inanimate movement - while executing action (Press, 2011). It is also worth noting that stimulus generalisation is a ubiquitous feature of associative learning (Pearce, 1987), which can explain the situations where inanimate movements activate mirror mechanisms (see Press et al., 2005), even to the same extent as human action. For example, as discussed in Section 2.1, when a mechanical stimulus presents similar joint configurations to a human body, tuning according to form may not be observed because all stimuli equally activate the sensory representation of action.

This account makes two predictions about biological tuning. First, correlated sensorimotor experience with inanimate movement should eliminate the tuning. Two studies support this hypothesis. Press et al. (2007) measured automatic imitation effects with human and robotic hand movements before any training, and, supporting previous findings (Press et al., 2006, 2005), found that the human stimuli generated larger automatic imitation effects than the robotic stimuli. Participants were subsequently trained with the robotic hands in a compatible (requiring performance of actions which matched those observed) or incompatible (requiring non-matching actions) fashion. Following such training, the group that had received incompatible training still exhibited greater automatic imitation of the human than robotic hands. However, the group that had received compatible training displayed equal automatic imitation of the two stimulus types. Cross et al. (2009) similarly found evidence that motor cortical areas were not biologically tuned following training with non-biological stimuli. During training, participants were required to perform dance step movements in response to an observed sequence of arrows. The arrows were accompanied (human present) or not (human

absent) by a video of a human executing these actions. The cortical response was subsequently measured with fMRI while participants observed the human present and human absent videos. This study demonstrated greater right premotor and pIFG (BA6 and BA44) cortical activation when participants observed the sequences with which they had associated actions during training, but no effect of whether there was a human present in the video or not. Therefore, presenting correlated sensorimotor experience with non-biological stimuli appears to eliminate the bias.

The second prediction states that the same representations in motor regions both mirror observed actions *and* respond to any other stimuli that have been paired predictively with action i.e. the *same* mechanisms both mediate action observation-execution mapping and arbitrary stimulus observation-execution mapping. We are exposed to a plethora of sensorimotor experience within our sensory world that does not relate to perceived action, or even perceived movement. For example, we swing a cricket bat on the right of our body, hear the sound of the ball contacting the bat in our right ear, and observe the ball rapidly appear from the right. Additionally, we observe objects such as teacups and learn to perform precision grips in their presence. We are also exposed to apparently arbitrary relationships between action and the physical sensory environment, for example, stamping on a brake pedal with our right foot when we see a red traffic light. After events have been paired systematically, we will automatically activate motor codes for grasping when we observe cups, or right foot movement in the presence of red lights, demonstrated by priming / interference effects with object-action pairs similar to that with observed-executed actions (Tucker and Ellis, 1998). Additionally, patients with prefrontal lesions who are impaired in top-down control exhibit utilisation behaviours with objects, whereby they will brush their teeth whenever they see a

toothbrush, as well as imitate actions in a way that is typically inhibited (Lhermitte et al., 1986).

Press et al. (2012a) conducted an fMRI study to test the hypothesis that the same mechanisms mediate action observation-execution mapping and arbitrary stimulus observation-execution mapping. During training arbitrary shapes such as hexagons, circles and squares were paired with executed manual intransitive actions such as hand splaying and thumb extension. There was no meaningful relationship between actions and shapes with which they were paired, and the specific shape-action combinations were counterbalanced between participants to control for any arbitrary pre-existing relationships not evident to the experimenters. After training, this study used adaptation techniques to demonstrate that shapes activated, not only motor, but specifically mirror representations of the actions with which they had been paired in training in right pIFG (BA44). The authors reached this conclusion via the following logic: First, participants could not observe their actions during training, therefore if common representations are activated when simply observing action and shapes with which the actions have been paired, it must be due to the shapes activating mirror (not purely motor) representations of action. Second, adaptation logic specifies that repeated activation of the same population of cells results in a decline in responsivity (Grill-Spector et al., 2006), and observation of a shape just after observation of the action with which the shape had been paired in training resulted in a reduced BOLD signal in BA44. Therefore, this study confirmed the hypothesis that the mechanisms involved in mirroring human action are not distinct from those that retrieve motor codes to other sensory events with which a predictive relationship has been established.

In conclusion, according to the domain-general associative account and a handful of recent findings, the same mechanisms that mediate mirroring of observed human action support retrieval of motor codes linked with other physical events in the environment. Therefore, mirror mechanisms must be considered one component of a domain-general system mapping between perceptual and motor domains to support a range of functions for action control. Under this hypothesis, biological tuning is not an intrinsic property of mirror mechanisms, but simply reflects the nature of an individual's sensorimotor experience.

4 Conclusion

A range of behavioural and neuroimaging studies demonstrate that we mirror observed human action to a greater extent than similar non-biological movement; tuning sensitive both to the form and the kinematic profile of observed movement. Biological tuning of mirror mechanisms may contribute to greater imitation of human action than inanimate movement, and a greater role of the motor system in perception of conspecifics. However, current evidence suggests that mirror mechanisms are one component of a domain-general system mapping between perception and action to support action control, and biological tuning reflects simply the nature of an individual's sensorimotor experience rather than an intrinsic property of the mechanism.

REFERENCES

Bird, G., Leighton, J., Press, C., Heyes, C., 2007. Intact automatic imitation of human and robot actions in autism spectrum disorders. Proc. R. Soc. B Biol. Sci. 274, 3027–3031. doi:10.1098/rspb.2007.1019

Brass, M., Bekkering, H., Prinz, W., 2001. Movement observation affects movement execution in a simple response task. Acta Psychol. (Amst.) 106, 3–22. doi:10.1016/S0001-6918(00)00024-X

Brass, M., Schmitt, R.M., Spengler, S., Gergely, G., 2007. Investigating Action Understanding: Inferential Processes versus Action Simulation. Curr. Biol. 17, 2117–2121. doi:10.1016/j.cub.2007.11.057

Candidi, M., Urgesi, C., Ionta, S., Aglioti, S.M., 2008. Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions. Soc. Neurosci. 3, 388–400. doi:10.1080/17470910701676269

Casile, A., Dayan, E., Caggiano, V., Hendler, T., Flash, T., Giese, M.A., 2010. Neuronal Encoding of Human Kinematic Invariants during Action Observation. Cereb. Cortex 20, 1647–1655. doi:10.1093/cercor/bhp229

Catmur, C., Walsh, V., Heyes, C., 2009. Associative sequence learning: the role of experience in the development of imitation and the mirror system. Philos. Trans. R. Soc. B Biol. Sci. 364, 2369–2380. doi:10.1098/rstb.2009.0048

Chaminade, T., Cheng, G., 2009. Social cognitive neuroscience and humanoid robotics. J. Physiol.-Paris 103, 286–295. doi:10.1016/j.jphysparis.2009.08.011

Chaminade, T., Franklin, D.W., Oztop, E., Cheng, G., 2005. Motor interference between Humans and Humanoid Robots: Effect of Biological and Artificial Motion, in: The 4th International Conference on Development and Learning, 2005. Proceedings. Presented at the The 4th International Conference on Development and Learning, 2005. Proceedings, pp. 96–101. doi:10.1109/DEVLRN.2005.1490951

Chartrand, T.L., Bargh, J.A., 1999. The chameleon effect: The perception–behavior link and social interaction. J. Pers. Soc. Psychol. 76, 893–910. doi:10.1037/0022-3514.76.6.893

Chong, T.T.-J., Cunnington, R., Williams, M.A., Mattingley, J.B., 2009. The role of selective attention in matching observed and executed actions. Neuropsychologia 47, 786–795. doi:10.1016/j.neuropsychologia.2008.12.008

Cisek, P., Kalaska, J.F., 2004. Neural correlates of mental rehearsal in dorsal premotor cortex. Nature 431, 993–996. doi:10.1038/nature03005

Cook, J., Swapp, D., Pan, X., Bianchi-Berthouze, N., Blakemore, S.-J., 2014. Atypical interference effect of action observation in autism spectrum conditions. Psychol. Med. 44, 731–740. doi:10.1017/S0033291713001335

Cook, R., Bird, G., Catmur, C., Press, C., Heyes, C., 2014. Mirror neurons: From origin to function. Behav. Brain Sci.

Costantini, M., Galati, G., Ferretti, A., Caulo, M., Tartaro, A., Romani, G.L., Aglioti, S.M., 2005. Neural Systems Underlying Observation of Humanly Impossible Movements: An fMRI Study. Cereb. Cortex 15, 1761–1767. doi:10.1093/cercor/bhi053

Cross, E.S., Hamilton, A.F. de C., Kraemer, D.J.M., Kelley, W.M., Grafton, S.T., 2009. Dissociable substrates for body motion and physical experience in the human action observation network. Eur. J. Neurosci. 30, 1383–1392. doi:10.1111/j.1460-9568.2009.06941.x

Cross, E.S., Liepelt, R., de C. Hamilton, A.F., Parkinson, J., Ramsey, R., Stadler, W., Prinz, W., 2012. Robotic movement preferentially engages the action observation network. Hum. Brain Mapp. 33, 2238–2254. doi:10.1002/hbm.21361

Dayan, E., Casile, A., Levit-Binnun, N., Giese, M.A., Hendler, T., Flash, T., 2007. Neural representations of kinematic laws of motion: Evidence for action-perception coupling. Proc. Natl. Acad. Sci. 104, 20582–20587. doi:10.1073/pnas.0710033104

De Lange, F.P., Spronk, M., Willems, R.M., Toni, I., Bekkering, H., 2008. Complementary Systems for Understanding Action Intentions. Curr. Biol. 18, 454–457. doi:10.1016/j.cub.2008.02.057

Di Dio, C., Gallese, V., 2009. Neuroaesthetics: a review. Curr. Opin. Neurobiol. 19, 682–687.

Dushanova, J., Donoghue, J., 2010. Neurons in primary motor cortex engaged during action observation. Eur. J. Neurosci. 31, 386–398. doi:10.1111/j.1460-9568.2009.07067.x

Engel, A., Burke, M., Fiehler, K., Bien, S., Rösler, F., 2008. How moving objects become animated: The human mirror neuron system assimilates non-biological movement patterns. Soc. Neurosci. 3, 368–387. doi:10.1080/17470910701612793

Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. Brain 119, 593–609. doi:10.1093/brain/119.2.593

Gallese, V., Gernsbacher, M.A., Heyes, C., Hickok, G., Iacoboni, M., 2011. Mirror Neuron Forum. Perspect. Psychol. Sci. 6, 369–407. doi:10.1177/1745691611413392

Gallese, V., Sinigaglia, C., 2011. What is so special about embodied simulation? Trends Cogn. Sci. 15, 512–519. doi:10.1016/j.tics.2011.09.003

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. doi:10.1016/j.neuroimage.2007.02.003

Gobbini, M.I., Gentili, C., Ricciardi, E., Bellucci, C., Salvini, P., Laschi, C., Guazzelli, M., Pietrini, P., 2011. Distinct neural systems involved in agency and animacy detection. J. Cogn. Neurosci. 23, 1911–1920. doi:10.1162/jocn.2010.21574

Goldenberg, G., Karnath, H.-O., 2006. The Neural Basis of Imitation is Body Part Specific. J. Neurosci. 26, 6282–6287. doi:10.1523/JNEUROSCI.0638-06.2006

Gowen, E., Bradshaw, C., Galpin, A., Lawrence, A., Poliakoff, E., 2010. Exploring visuomotor priming following biological and non-biological stimuli. Brain Cogn. 74, 288–297. doi:10.1016/j.bandc.2010.08.010

Gowen, E., Stanley, J., Miall, R.C., 2008. Movement interference in autism-spectrum disorder. Neuropsychologia 46, 1060–1068. doi:10.1016/j.neuropsychologia.2007.11.004

Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn. Sci. 10, 14–23. doi:10.1016/j.tics.2005.11.006

Heiser, M., Iacoboni, M., Maeda, F., Marcus, J., Mazziotta, J.C., 2003. The essential role of Broca's area in imitation. Eur. J. Neurosci. 17, 1123–1128. doi:10.1046/j.1460-9568.2003.02530.x

Heyes, C.M., 1993. Imitation, culture and cognition. Anim. Behav. 46, 999–1010. doi:10.1006/anbe.1993.1281

Hogan, N., 1984. An organizing principle for a class of voluntary movements. J. Neurosci. 4, 2745–2754.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G., 2005. Grasping the Intentions of Others with One's Own Mirror Neuron System. PLoS Biol 3, e79. doi:10.1371/journal.pbio.0030079

Kilner, J., Hamilton, A.F. de C., Blakemore, S.-J., 2007. Interference effect of observed human movement on action is due to velocity profile of biological motion. Soc. Neurosci. 2, 158–166. doi:10.1080/17470910701428190

Kilner, J.M., Neal, A., Weiskopf, N., Friston, K.J., Frith, C.D., 2009. Evidence of Mirror Neurons in Human Inferior Frontal Gyrus. J. Neurosci. 29, 10153–10159. doi:10.1523/JNEUROSCI.2668-09.2009

Kilner, J.M., Paulignan, Y., Blakemore, S.., 2003. An interference effect of observed biological movement on action. Curr. Biol. 13, 522–525. doi:10.1016/S0960-9822(03)00165-9

Klapper, A., Ramsey, R., Wigboldus, D., Cross, E.S., 2014. The Control of Automatic Imitation Based on Bottom–Up and Top–Down Cues to Animacy: Insights from Brain and Behavior. J. Cogn. Neurosci. 1–11. doi:10.1162/jocn_a_00651

Kupferberg, A., Huber, M., Helfer, B., Lenz, C., Knoll, A., Glasauer, S., 2012. Moving Just Like You: Motor Interference Depends on Similar Motility of Agent and Observer. PLoS ONE 7, e39637. doi:10.1371/journal.pone.0039637

Lacquaniti, F., Terzuolo, C., Viviani, P., 1983. The law relating the kinematic and figural aspects of drawing movements. Acta Psychol. (Amst.) 54, 115–130. doi:10.1016/0001-6918(83)90027-6

Lhermitte, F., Pillon, B., Serdaru, M., 1986. Human autonomy and the frontal lobes. Part I: Imitation and utilization behavior: A neuropsychological study of 75 patients. Ann. Neurol. 19, 326–334. doi:10.1002/ana.410190404

Liepelt, R., Brass, M., 2010. Top-down modulation of motor priming by belief about animacy. Exp. Psychol. 57, 221–227. doi:10.1027/1618-3169/a000028

Lingnau, A., Gesierich, B., Caramazza, A., 2009. Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. Proc. Natl. Acad. Sci. 106, 9925–9930. doi:10.1073/pnas.0902262106

Longo, M.R., Bertenthal, B.I., 2009. Attention modulates the specificity of automatic imitation to human actors. Exp. Brain Res. 192, 739–744. doi:10.1007/s00221-008-1649-5

Marin, L., Issartel, J., Chaminade, T., 2009. Interpersonal motor coordination: From human–human to human–robot interactions. Interact. Stud. 10, 479–504. doi:10.1075/is.10.3.09mar

Miura, N., Sugiura, M., Takahashi, M., Sassa, Y., Miyamoto, A., Sato, S., Horie, K., Nakamura, K., Kawashima, R., 2010. Effect of motion smoothness on brain activity while observing a dance: An fMRI study using a humanoid robot. Soc. Neurosci. 5, 40–58. doi:10.1080/17470910903083256

Newman-Norlund, R.D., Ondobaka, S., van Schie, H.T., van Elswijk, G., Bekkering, H., 2010. Virtual Lesions of the IFG Abolish Response Facilitation for Biological and Non-Biological Cues. Front. Behav. Neurosci. 4. doi:10.3389/neuro.08.005.2010

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. doi:10.1016/j.neucom.2006.02.024

Oosterhof, N.N., Tipper, S.P., Downing, P.E., 2013. Crossmodal and action-specific: neuroimaging the human mirror neuron system. Trends Cogn. Sci. 17, 311–318. doi:10.1016/j.tics.2013.04.012

Pearce, J.M., 1987. A model for stimulus generalization in Pavlovian conditioning. Psychol. Rev. 94, 61–73. doi:10.1037/0033-295X.94.1.61

Pellegrino, G. di, Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G., 1992. Understanding motor events: a neurophysiological study. Exp. Brain Res. 91, 176–180. doi:10.1007/BF00230027

Press, C., 2011. Action observation and robotic agents: Learning and anthropomorphism. Neurosci. Biobehav. Rev. 35, 1410–1418.

Press, C., Bird, G., Flach, R., Heyes, C., 2005. Robotic movement elicits automatic imitation. Cogn. Brain Res. 25, 632–640. doi:10.1016/j.cogbrainres.2005.08.020

Press, C., Catmur, C., Cook, R., Widmann, H., Heyes, C., Bird, G., 2012a. fMRI Evidence of "Mirror" Responses to Geometric Shapes. PLoS ONE 7, e51934. doi:10.1371/journal.pone.0051934

Press, C., Cook, J., Blakemore, S.-J., Kilner, J., 2011. Dynamic modulation of human motor activity when observing actions. J. Neurosci. Off. J. Soc. Neurosci. 31, 2792–2800. doi:10.1523/JNEUROSCI.1595-10.2011

Press, C., Gillmeister, H., Heyes, C., 2006. Bottom-up, not top-down, modulation of imitation by human and robotic models. Eur. J. Neurosci. 24, 2415–2419. doi:10.1111/j.1460-9568.2006.05115.x

Press, C., Gillmeister, H., Heyes, C., 2007. Sensorimotor experience enhances automatic imitation of robotic action. Proc. R. Soc. B Biol. Sci. 274, 2509–2514. doi:10.1098/rspb.2007.0774

Press, C., Weiskopf, N., Kilner, J.M., 2012b. Dissociable roles of human inferior frontal gyrus during action execution and observation. NeuroImage 60, 1671–1677. doi:10.1016/j.neuroimage.2012.01.118

Rizzolatti, G., Craighero, L., 2004. THE MIRROR-NEURON SYSTEM. Annu. Rev. Neurosci. 27, 169–192. doi:10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., Fadiga, L., 1998. Grasping objects and grasping action meanings: the dual role of monkey rostroventral premotor cortex (area F5). Novartis Found. Symp. 218, 81–95; discussion 95–103.

Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and the recognition of motor actions. Cogn. Brain Res. 3, 131–141. doi:10.1016/0926-6410(95)00038-0

Saygin, A.P., Wilson, S.M., Hagler, D.J., Bates, E., Sereno, M.I., 2004. Point-Light Biological Motion Perception Activates Human Premotor Cortex. J. Neurosci. 24, 6181–6188. doi:10.1523/JNEUROSCI.0504-04.2004

Shimada, S., 2010. Deactivation in the sensorimotor area during observation of a human agent performing robotic actions. Brain Cogn. 72, 394–399. doi:10.1016/j.bandc.2009.11.005

Stanley, J., Gowen, E., Miall, R.C., 2007. Effects of agency on movement interference during observation of a moving dot stimulus. J. Exp. Psychol. Hum. Percept. Perform. 33, 915–926. doi:10.1037/0096-1523.33.4.915

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. doi:10.1016/j.neuroimage.2010.04.025

Stevens, J.A., Fonlupt, P., Shiffrar, M., Decety, J., 2000. New aspects of motion perception: selective neural encoding of apparent human movements. Neuroreport 11, 109–115.

Tai, Y.F., Scherfler, C., Brooks, D.J., Sawamoto, N., Castiello, U., 2004. The Human Premotor Cortex Is "Mirror" Only for Biological Actions. Curr. Biol. 14, 117–120. doi:10.1016/j.cub.2004.01.005

Tucker, M., Ellis, R., 1998. On the relations between seen objects and components of potential actions. J. Exp. Psychol. Hum. Percept. Perform. 24, 830–846. doi:10.1037/0096-1523.24.3.830

BOX 1: Beliefs about stimulus identity

Stanley et al. (2007) examined effects of instructing participants that stimuli were human or computer generated, when the stimuli were in fact identical, to test effects of belief about stimulus identity on mirror activation. They found a larger interference effect when participants were instructed that dot stimuli were generated by a human rather than a computer, regardless of whether the dots moved with a human or constant velocity profile. However, in contrast, Press et al. (2006) found no evidence of effects of belief. In an automatic imitation factorial design, participants saw human or robotic hand movements, and were instructed in one session that these were human generated, and in another, that they were performed by a robot. There was no effect of instruction on automatic imitation, either when the stimuli had physically human or robotic properties. Instead, the effects were determined by the stimulus perceptual properties, with a larger automatic imitation effect for human relative to robotic hands. This lack of instruction effect was observed despite questionnaire measures indicating that beliefs about identity had been successfully manipulated.

There are at least two possible explanations for the discrepancy between findings in these studies. First, there was arguably more perceptual information about animacy in Press et al. (2006) than Stanley et al. (2007) and belief about identity may have an impact only when there is little perceptual information upon which to base inferences. This 'perception hypothesis' is consistent with an fMRI experiment conducted by Stanley et al. (2010), where 15 points, rather than one (Stanley et al., 2007), constituted the perceptual information. There was no difference in activation in any motor, premotor, or pIFG cortical areas regardless of whether participants were told that the stimulus was human or computer generated (N.B. However, this study also did not find any motor effects that correlated with the level of actual human motion in the

stimulus). Second, participants had more control over the locus of their spatial attention in Stanley et al. (2007) than Press et al. (2006), and greater attention to stimuli believed to be human may generate belief effects. More attention to stimuli has been found to lead to larger automatic imitation effects (Chong et al., 2009; see also Gowen et al., 2010; Longo and Bertenthal, 2009), and in Stanley et al.'s study (2007) participants were not required to devote high attention to the stimuli; they only needed to pace their actions with observed stimuli and the pace was constant. In contrast, Press et al. (2006) required participants to respond on the basis of stimulus movement, where this movement happened at a variable point in the trial, and the task was to respond as quickly as possible. Therefore, attention towards stimuli may have been high regardless of belief. This 'attention hypothesis' – that greater attention to stimuli believed to be human than inanimate generates belief effects – is supported by a study which found effects of belief on automatic imitation when there was high perceptual information, but the response was not signalled by the observed action meaning that attention was free to shift (Liepelt and Brass, 2010; see also Klapper et al., 2014).

If the perception hypothesis is correct, beliefs may indeed exert direct top-down influence on the operation of mirror mechanisms. In contrast, if the attention hypothesis is found to provide a better account of the data, beliefs would not directly determine the operation of mirror mechanisms – beliefs act upon mechanisms determining spatial attention, and level of perceptual processing therefore impacts upon the operation of mirror mechanisms (as well as many other sociocognitive processes). Hence, given the uncertainty about the nature of differences between studies, there is currently no evidence that beliefs about identity play a direct role in biological tuning.

BOX 2: Future directions

1. Using neuroimaging techniques that can demonstrate specificity - and therefore that motor codes mirror - do all of these outlined motor cortical regions reflect biological tuning? Are different regions sensitive to form and kinematic information?

2. Does belief about stimulus identity directly influence operation of mirror mechanisms (Box 1), and if so, how do these top-down influences interact with the level of activation according to stimulus properties?

3. What is the role of mirror mechanisms in intentional imitation and perception, and how does biological tuning influence these functions with human and inanimate stimuli?

4. Does the origin and function of mirror mechanisms equate entirely to that of other perceptual-motor mapping mechanisms, for example, those mapping simple spatial coordinates?

FIGURE LEGENDS

Figure 1. Behavioural measures of mirror mechanism operation during action observation. (a) The interference procedure used by Kilner et al. (2003). Participants must execute sinusoidal vertical or horizontal arm actions at the same time as observing vertical or horizontal actions in phase with the executed actions. The observed actions (e.g. horizontal) can either be in the same or opposite direction as executed actions. Variance in the dimension perpendicular to intended motion in the executed actions is recorded. This variance is higher when observing actions perpendicular to the intended execution direction. (b) The automatic imitation procedure used by Brass et al. (2001). In a simple RT task, participants are presented with a hand in a neutral position. After a certain amount of time, the stimulus hand moves (e.g. the finger lifts). Participants are instructed to execute a pre-specified response upon movement of the stimulus hand. This pre-specified response can either be compatible (finger lifting) or incompatible (finger tapping) with the observed movement. The automatic imitation effect is calculated by subtracting RT on compatible trials from RT on incompatible trials.

Figure 2. Form manipulations. (a) Human and robot form stimuli used in Press et al. (2005). (b) Humanoid robot form stimulus used in Kupferberg et al. (2012). (c) Human and Lego form stimuli used in Cross et al. (2012). Note that biological tuning was only observed in (a) where the joint configurations of the robotic stimulus are different from a human hand.

(a)

Stimulus   Response   Stimulus   Response

Compatible   Incompatible

Stimulus   Response

(b)

Compatible

Incompatible

(a)

(b)

forearm

joint 5
axis

joint 4
axis

hand

joint 6
axis

elbow

joint 3
axis

upper arm

joint 1
axis

shoulder

joint 2
axis

base

(c)