



Review

Action observation and robotic agents: Learning and anthropomorphism

Clare Press^{a,b,*}^a Wellcome Trust Centre for Neuroimaging, Institute of Neurology, University College London, 12 Queen Square, London WC1N 3BG, United Kingdom^b School of Psychology and Clinical Language Sciences, University of Reading, Whiteknights, Reading RG6 6AL, United Kingdom

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ABSTRACT

The 'action observation network' (AON), which is thought to translate observed actions into motor codes required for their execution, is biologically tuned: it responds more to observation of human, than non-human, movement. This biological specificity has been taken to support the hypothesis that the AON underlies various social functions, such as theory of mind and action understanding, and that, when it is active during observation of non-human agents like humanoid robots, it is a sign of ascription of human mental states to these agents. This review will outline evidence for biological tuning in the AON, examining the features which generate it, and concluding that there is evidence for tuning to both the form and kinematic profile of observed movements, and little evidence for tuning to belief about stimulus identity. It will propose that a likely reason for biological tuning is that human actions, relative to non-biological movements, have been observed more frequently while executing corresponding actions. If the associative hypothesis of the AON is correct, and the network indeed supports social functioning, sensorimotor experience with non-human agents may help us to predict, and therefore interpret, their movements.

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1. Introduction

Observation of actions activates the motor codes required for their performance. For example, it has been shown behaviourally that we automatically imitate others, when there is no intention to

have done so, and no reported awareness of having done so (e.g. Chartrand and Bargh, 1999). In line with such behavioural data, neuroimaging studies have shown that observing action activates an 'action observation network', including ventral and dorsal premotor cortices, primary motor cortex, and inferior parietal lobule (Rizzolatti et al., 1996; Buccino et al., 2001; Grezes and Decety, 2001; Gazzola and Keysers, 2008; Kilner et al., 2009). Some of these areas, namely ventral premotor cortex and inferior parietal lobule, correspond to those in which 'mirror neurons' have been found in the macaque monkey: These neurons discharge not only when the monkey executes an action of a certain type (e.g. precision grip),

* Corresponding author at: School of Psychology and Clinical Language Sciences, University of Reading, Whiteknights, Reading RG6 6AL, United Kingdom.
Tel.: +44 0 118 378 5450.

E-mail address: c.m.press@reading.ac.uk

but also when it observes the experimenter performing that action (Di Pellegrino et al., 1992; Gallese et al., 1996, 2002; note that neurons with similar properties have also been found in primary motor cortex and dorsal premotor cortex (Cisek and Kalaska, 2004; Dushanova and Donoghue, 2010)).

The AON is biologically tuned, such that it responds more to the observation of human, than non-human, movement (either defined by form or kinematic profile). This biological tuning may be crucial for sociocognitive functioning, which the AON is hypothesized to support (e.g. Gallese and Goldman, 1998). On the basis of such hypotheses, some have suggested that when the AON is active during the observation of non-human agents like humanoid robots, it is a sign of the ascription of human properties such as mental states to these agents (e.g. Oberman et al., 2007; Gazzola et al., 2007; Chaminade and Cheng, 2009). For example, Oberman et al. (2007) claim that '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 . . . (AON activation) indicates the extent to which an artificial agent is considered as a social inter-actor' (p. 289).

This review will outline evidence of biological tuning in the AON. It will consider the AON to be a mechanism which translates an observed action into motor codes required for execution. It will therefore cover behavioural studies indicating operation of such translation processes (see Heyes, *in press*) and neurological studies suggesting activation of components of the motor network when observing actions, including primary motor cortex, and ventral and dorsal premotor cortices; both BA6 and BA44. This range of coverage is not assuming that activations in different components of the motor network will all necessarily signal the same processes; it simply reflects that, on the basis of present theorizing about the AON, the components cannot be divided functionally with confidence. It will examine the features of observed actions which generate biological specificity, and conclude that there is evidence for tuning to both the form and kinematic profile of observed movements, and little evidence for direct tuning to belief about identity. It will subsequently propose that biological tuning in the AON is a result of more frequent and systematic observation of human actions while executing corresponding actions. If the AON develops through learning, and it indeed supports social functions such as action understanding, sensorimotor experience with agents may help us to predict, and therefore interpret, their movements.

2. Biological tuning in the AON

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 interference 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. Imaging studies support these behavioural findings: A positron emission tomography (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). Furthermore, in three functional magnetic resonance imaging (fMRI) studies, stronger premotor 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).

However, there are at least two differences between the human and non-human stimuli presented in these five experiments. First, the stimuli differ in form. Namely, the human stimuli are a flesh colour and rounded, whereas the non-biological stimuli are often more geometric. Second, the stimuli differ in kinematics. The human arms have followed an approximately minimum jerk trajectory, where the movement is slow at turning points and speeds up on straighter trajectories (Hogan, 1984). The non-biological stimuli have tended to move 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 specificity within the AON.

2.1. Biological tuning evidence: influence of form

In a simple reaction time (RT) task, Brass et al. (2001) found evidence of greater AON activation when stimuli had a human, rather than square, form, and stimuli 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. Brass et al. (2001) found no evidence of an automatic imitation effect when responses were made to a square that moved up or down with the same kinematic profile as the observed finger actions. 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. An electroencephalography (EEG) study has indicated that these behavioural effects may result from differences in processing in motor circuits: Oberman et al. (2005) found greater attenuation of *mu* frequency oscillations over sensorimotor electrodes – a signature of sensorimotor cortex activation – when participants observed videos of hand movements rather than balls which moved with the same kinematics. Additionally, a magnetoencephalography (MEG) study demonstrated differential processing in ventral premotor cortex when observing and imitating finger movements rather than points moving with similar kinematics (Kessler et al., 2006; Biermann-Ruben et al., 2008; cf. Jonas et al., 2007).

Influences of form on AON activation have also been found when the non-human stimuli are more similar to the human stimuli. Perani et al. (2001) found activation in left BA6 when participants observed real human hand grasping actions, but not when observing a virtual reality hand moving with the same kinematics. In addition, Press et al. (2005) investigated differences in processing of human and robotic form, while controlling for kinematics, by

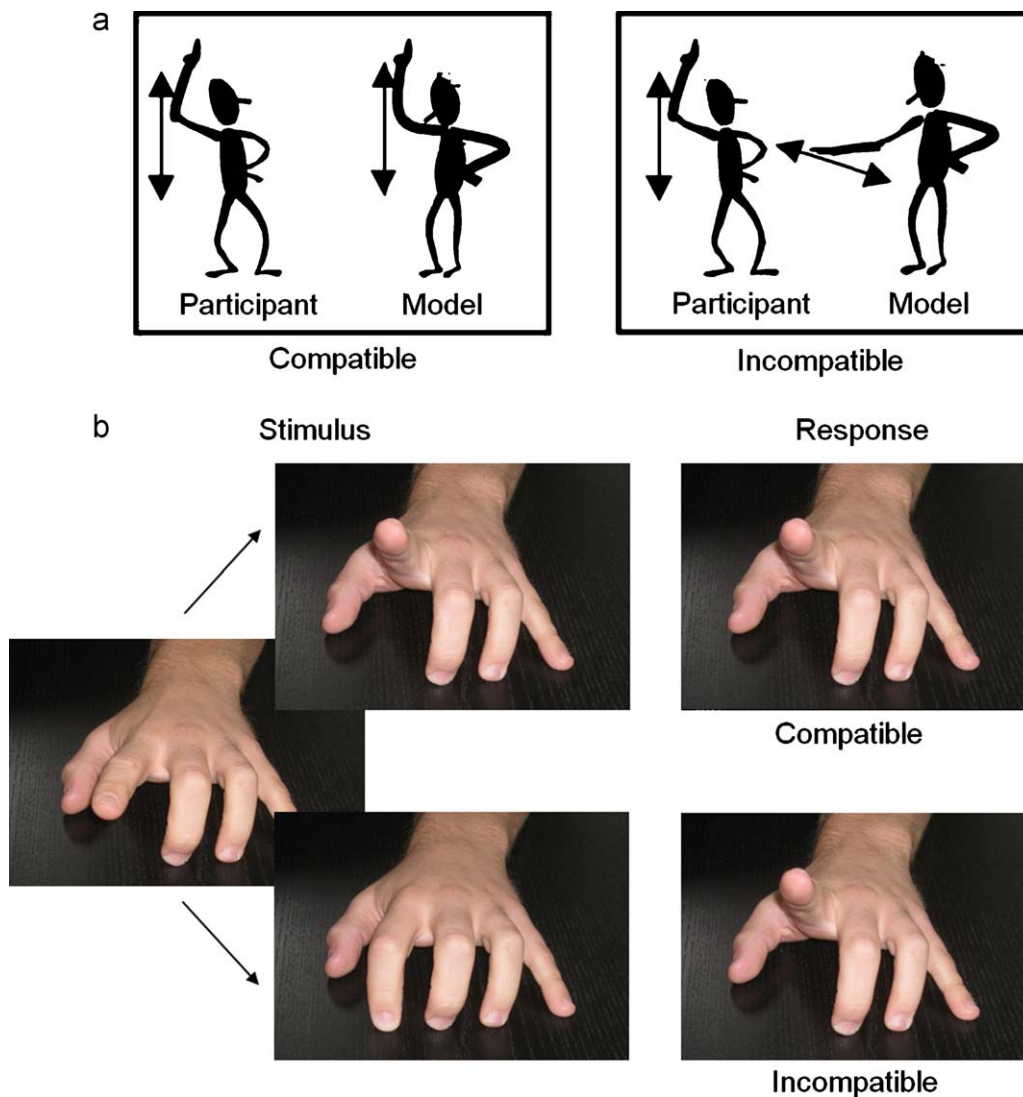


Fig. 1. Behavioural indices of AON activation during action observation. (a) The interference procedure used by Kilner et al. (2003). Participants must execute sinusoidal vertical or horizontal arm actions at the same time as observing vertical or horizontal actions in phase with the executed actions. 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.

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 half-open, half-closed, 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 Press et al., 2006, 2007; Bird et al., 2007, for the same effect). These studies therefore indicate that stimuli with human form activate the AON to a greater degree than stimuli with closely matched non-biological form.

2.2. Biological tuning evidence: influence of kinematics

Other studies have examined the effects of kinematics on AON activation. Behavioural studies have indicated that, when stimuli

are matched for form, movements with human kinematics generate greater AON activation than movements with non-biological kinematics. For example, Kilner et al. (2007a) found larger behavioural interference effects when participants observed human form stimuli that moved with human kinematics rather than constant velocity (cf. Gowen et al., 2008). Chaminade et al. (2005) similarly found more interference when a humanoid robot form stimulus moved with human kinematics rather than an artificially generated trajectory. In addition, Longo et al. (2008) found greater automatic imitation effects when fingers moved in a kinematically plausible fashion, compared with conditions where the combination of joint movements was impossible to produce (Experiment 2, cf. Costantini et al., 2005; Romani et al., 2005; Cross et al., 2010, where greater AON activation is not found for possible relative to impossible actions). Furthermore, Candidi et al. (2008) demonstrated that transcranial magnetic stimulation over ventral premotor cortex (BA44) impaired the ability of participants to discriminate two kinematically possible arm and leg actions, but had no effect on

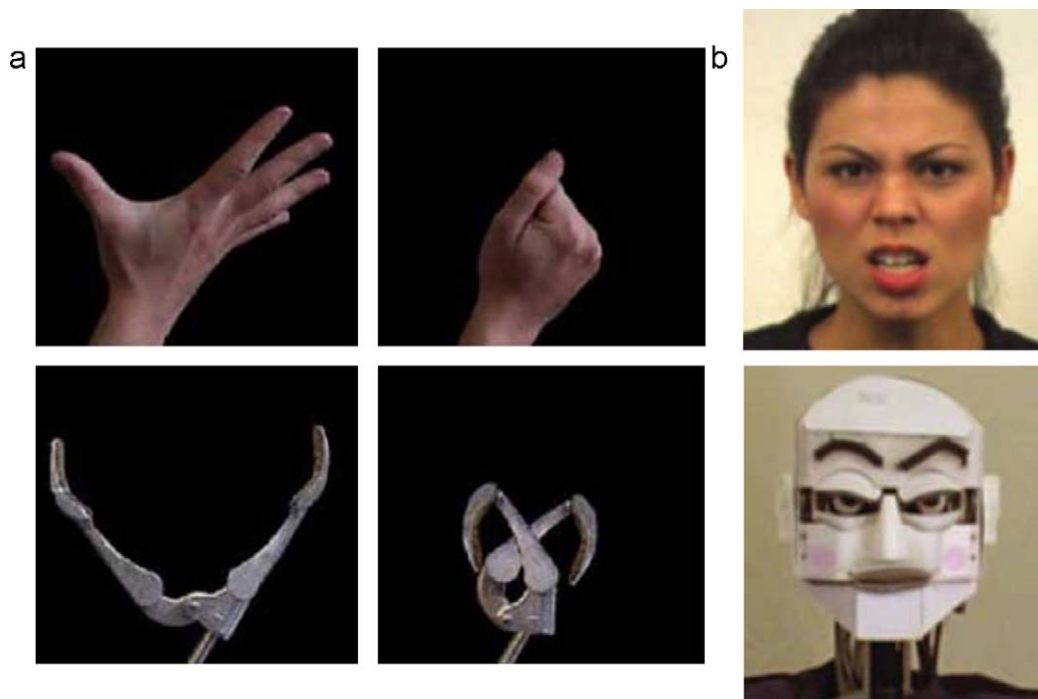


Fig. 2. Form manipulations. (a) Human and robot form stimuli used in Press et al. (2005). (b) Human and humanoid robot form stimuli used in Gobbini et al. (in press).

their performance in distinguishing two kinematically impossible movements.

In line with these behavioural data, a virtual reality near-infrared spectroscopy study showed 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 observed a similar pattern: 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, sensorimotor activation 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 in neuroimaging studies when the non-biological kinematic profile is matched to the human profile for complexity (see Gazzola et al., 2007). One PET study (Stevens et al., 2000) showed greater primary motor 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 – activates premotor structures to a greater extent than observing movements with the inverted kinematic profile. These studies therefore indicate clearly that stimuli with human kinematics activate the AON to a greater extent than stimuli with non-biological kinematics.

2.3. Effects of belief 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 provide a test of effects of belief about

stimulus identity. 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 evidence of effects of instruction on the magnitude of automatic imitation effects, either when the stimuli had physically human or robotic properties. Instead, the effects were driven by the perceptual properties of the stimuli, such that there was a larger automatic imitation effect with human relative to robotic hands. This lack of instruction effect was observed despite questionnaire measures indicating that beliefs about identity had been successfully manipulated.

The discrepancy between the findings of Press et al. (2006) and Stanley et al. (2007) needs further exploration, but it is possible that Stanley et al. (2007) observed effects of belief because there was very little perceptual information (i.e. points moving rather than more complex forms). Belief about identity may have greater impact when there is less perceptual information upon which to base inferences. This explanation of experimental differences 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 or premotor 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/premotor effects that correlated with the level of actual human motion in the stimulus). Alternatively, greater attention to stimuli believed to be human may have generated the effects of belief in Stanley et al. (2007); more attention to stimuli has been found to lead to larger automatic imitation effects (Chong et al., 2009; see also Longo and Bertenthal, 2009; Gowen et al., 2010). In the experiment of Stanley et al. (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. Attention towards stimuli may have been high regardless of belief in this experiment. This explanation is supported by a recent study which found effects of belief on automatic imitation when there was a reasonable amount of perceptual information, but where the response was not signalled by the observed action (Liepelt and Brass, 2010).

2.4. Studies failing to find biological tuning

One fMRI study observed equal AON 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 and BA45 coordinates). Gazzola et al. (2007) considered that these findings may be explained if assuming that the AON only encodes the 'goal' of observed actions, for example, reaching for an object, and not how that is achieved. However, it is unlikely that the AON, as a whole, is only sensitive to 'goal' features due to the large number of studies outlined above which indicate sensitivity to form and kinematics. Of course, future research must establish whether different components of the network are sensitive to different features (see Hamilton and Grafton, 2007).

Additionally, three studies have indicated little difference in AON activation when observing human and humanoid robot actions (Oztop et al., 2005; Oberman et al., 2007; Gobbini et al., *in press*; see also Liepelt et al., 2010). Oztop et al. (2005) found similar behavioural interference effects with arm movements when observing human and humanoid stimuli. Oberman et al. (2007) found equal *mu* suppression effects when observing human and humanoid opening and closing hand movements, and Gobbini et al. (*in press*) (see Fig. 2b) 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). In these studies, the form of humanoid robots is matched approximately to that of a human, with a broadly compatible arrangement of body parts. Additionally, the robots move with an approximately human kinematic profile. Therefore, it could be assumed that there are potential differences to be observed between these human and humanoid stimuli, but that measures of AON activation are not sufficiently sensitive to detect them; an argument lent further support by the study of Chaminade et al. (2010), which suggests that differences may be found when observing human and humanoid speech gestures.

2.5. Biological tuning evidence: conclusion

In summary, there have been a number of studies indicating greater AON activation when observing human stimuli, relative to non-human stimuli. There are observable influences both of the form and the kinematics of the stimuli. There is little evidence of a direct influence of belief about the identity of the observed stimulus.

3. Origin of biological tuning in the AON

3.1. Theories about the origin of biological tuning

There are two prominent theories concerning the origins of the AON. The first posits that the network evolved through natural selection to support higher level sociocognitive functioning, such as theory of mind (Gallese and Goldman, 1998; Rizzolatti

and Sinigaglia, 2010). In contrast, the associative sequence learning model (ASL, e.g. Heyes, 2001, 2010) suggests that the AON acquires its mirror properties through sensorimotor learning (see Chaminade et al., 2008 for a simulation). Experience in which observation of an action is correlated with its execution establishes excitatory links between sensory and motor representations of the same action, and these mediate AON activation (see Fig. 3, N.B. Ideomotor theory makes similar predictions about the origin of the AON for perceptually transparent actions; Brass and Heyes, 2005; Massen and Prinz, 2009). There is ample opportunity for such learning, for example, when observing our own actions, when caregivers imitate us, and when responding in the same way as others to an external event (Ray and Heyes, 2011).

Both of these hypotheses are consistent with the finding that the observation of human actions activates the AON to a greater extent than the observation of non-biological movements: if the AON evolved through natural selection to support inferences about mental states, it should not be tuned to the movements of non-biological systems which lack mental states. Similarly, if the AON emerges through correlated sensorimotor experience, one would expect biological tuning because self-observation, mirrors and synchronous social activities ensure that there are many more opportunities in the course of human development to execute actions while observing the same human actions than while observing similar non-biological movements (see Ray and Heyes, 2011).

ASL predicts that human stimuli will typically activate the AON more than non-human stimuli, for the reasons outlined above; it does not predict that the AON will be inactive when observing non-human stimuli. Stimulus generalisation is a ubiquitous feature of associative learning (Pearce, 1987); the effects of training with a stimulus, X, are not only present in behaviour in response to X, but also in behaviour elicited by other stimuli to the extent that those stimuli have physical characteristics in common with X. Therefore, ASL predicts that non-biological stimuli will still activate the AON to the extent that they are perceptually similar to the human stimuli with which humans have learned sensorimotor associations. This prediction is consistent with indications of AON activation when observing robotic movements which are clearly non-human (e.g. Press et al., 2005, 2006, 2007; Gazzola et al., 2007). Stimuli that are not at all human either in terms of form or kinematics may also activate components of the AON to the extent that the stimulus display overlaps perceptually with stimuli which have been associated with action (e.g. observation of a moving object which typically moves only during action, or observation of human-like movement trajectories; see Ramsey and Hamilton, 2010). However, this activation would be predicted to be usually lower than that elicited by human stimuli, which are likely to share greater perceptual similarity with stimuli associated with action (see Press et al., 2005 for a discussion). The natural selection hypothesis does not explicitly predict stimulus generalisation. However, some degree of stimulus generalisation may be consistent with this hypothesis, and for this reason, evidence of stimulus generalisation will not be considered, in this review, to favour the associative over the natural selection account.

3.2. Evidence concerning origin of biological tuning

Evidence of an AON in macaque monkeys – close genetic relatives to humans – has been proposed to support the natural selection account (Gallese and Goldman, 1998). However, this can only provide strong support if it can be demonstrated that macaques do not have experience of the type that could lead to the development of the AON through associative learning. No such evidence is currently available. In addition, evidence of human neonatal imitation, if solid, would provide good support for the natural selection account, given that there would have been little

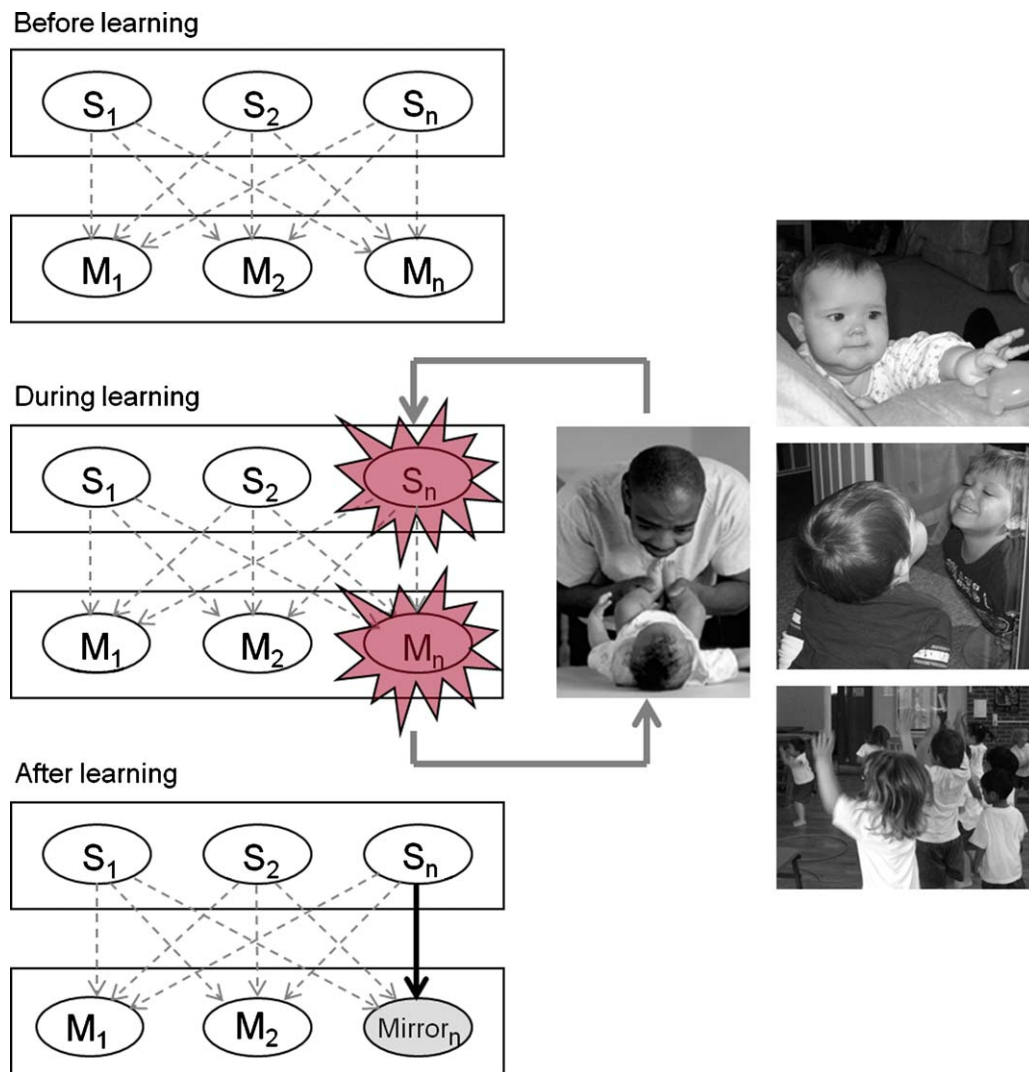


Fig. 3. Associative sequence learning theory. Sensory and motor representations of action are initially separate. Our developmental environment provides us with correlated activation of sensory and motor representations of the same action, leading to formation of sensorimotor links. Adapted from Heyes, 2010.

opportunity for associative learning as a neonate. There have been many studies claiming to find imitation in infants as young as a few hours old (e.g. Meltzoff and Moore, 1977, 1983, 1989). However, there may only be good evidence for neonatal imitation of tongue protrusion (Anisfeld, 1991, 1996) and even this may result from simple arousal (Jones, 1996, 2006) rather than AON functioning.

Effects of training and expertise within the AON support the associative learning hypothesis concerning its origin. Although the operation of innate systems could, in principle, be modified by experience, it has been argued that experience-based alteration of innate systems would usually be maladaptive, and therefore that natural selection is likely to have acted to prevent such modification (Pinker, 1997). In a similar vein, Lorenz (1966) states that inherited aspects of behaviour can be identified as the 'least changeable' (p. 35). Several studies have indicated effects of sensorimotor experience with human stimuli (e.g. Calvo-Merino et al., 2005; Heyes et al., 2005; Catmur et al., 2007) and that the effects of experience are dependent on those features which would be predicted by the associative model. For example, Cook et al. (2010) demonstrated that the influences of experience on automatic imitation were dependent on the 'contingency', or predictive relationship, between stimulus and response during training. During training, a

contingent group always opened their hand when they observed a hand close, and closed their hand when they saw a hand open. This regime presented non-matching experience of observed and executed actions, which the ASL model predicts will reduce automatic imitation effects. A non-contingent group experienced the same number of these trials, but an equal number of trials where they opened and closed their hand while a stimulus hand did not move. The effect of training was significantly reduced in the non-contingent group relative to the contingent group; the automatic imitation effect was larger in the non-contingent group following the non-matching training.

There are also two studies which indicate effects of experience on biological specificity. Press et al. (2007) measured automatic imitation effects with human and robotic hand movements before any training, and, supporting previous findings (Press et al., 2005, 2006), 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. This finding indicates equal AON activation when observing human and robotic movements following matching sensorimotor experience with robotic stimuli.

Cross et al. (2009) similarly found evidence that the AON was 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 either accompanied or not 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 stimuli. This study demonstrated greater right premotor (BA6 and BA44) cortical activation when participants observed the sequences which they had associated with motor responses during training, but no effect of whether there was a human present in the video or not.

These studies indicate that biological tuning within the AON is likely to result from greater opportunity to associate the observation of human movements with the execution of corresponding actions. Given such opportunity to associate actions with non-biological stimuli such as robots, there is evidence of equivalent AON activation when observing human and non-biological movements.

4. Anthropomorphism

It has been suggested that when the AON is active during the observation of non-human agents like humanoid robots, it is a sign of the ascription of human mental states to these agents (e.g. Gazzola et al., 2007). If the AON evolved through natural selection to support mental state inferences (Gallese and Goldman, 1998; Rizzolatti and Sinigaglia, 2010), that is, it is the function for which the network evolved, it may be possible to predict that its activation signals mental state inference. However, it should be noted that even under the natural selection hypothesis, the AON may not be sufficient to support mental state inference. Such assumptions also cannot be made under the associative hypothesis (Heyes, 2001, 2010). The network may support social functions such as theory of mind and action understanding once it is operational, but this functionality cannot be assumed (see Press et al., in press). Therefore, any claims that AON activation when observing robotic movement reflects ascription of human mental states and feelings to such robots are premature.

The hypothesis that the biological tuning within the AON reflects sensorimotor experience only suggests that claims that AON activation indicates ascription of human feelings and mental states are premature; not necessarily incorrect. It may be found that, whether mental state inference itself relies on the AON or not (Saxe, 2005; Brass et al., 2007; De Lange et al., 2008), AON activation may be a reliable predictor of ascription of mental states and/or feelings. Neurological and behavioural studies can answer this question by examining correlations between AON activation and subjective ratings of social qualities of observed agents.

Furthermore, if the AON is functionally involved in mental state inference, and the AON develops through associative learning, simple visual experience with non-human agents, correlated with action execution, may enhance our ability to predict, and therefore interpret, their movements. That is, such correlated experience could allow us to retrieve motor codes associated with observation of those non-human movements, and perhaps higher level mental states associated with the motor codes, and to use this information to aid prediction of what is seen (see Kilner et al., 2007b,c for a model of how we might perform this function when observing human actions). In all Western cultures, we are encountering vir-

tual agents more than ever, and in certain cultures, such as Japan, mechanical robots are also becoming widespread. However, realistic these agents become, it will be difficult to ever make them indistinguishable from humans. Therefore, it is of great importance to develop and enhance our ability to interact with these non-human agents (Chaminade and Hodgkins, 2006; Chaminade and Cheng, 2009; Chaminade and Kawato, 2010; Marin et al., 2009). By enhancing our ability to predict and interpret the movements of non-human agents, correlated sensorimotor experience with them may even help to overcome the problem of the 'uncanny valley' (e.g. Marin et al., 2009), whereby there is a negative emotional response to non-human agents that have realistic human-like, but imperfect, form and motion properties.

5. Conclusion

The present review has outlined evidence to suggest that the AON, which is thought to translate an observed action into the motor codes required for its execution, responds more to the observation of human, than non-human, movement. It examined the features which generate this biological specificity, and concluded that there is evidence for tuning to both the biological form and kinematic profile of observed movements. It found little evidence for tuning to beliefs about stimulus identity. It subsequently posited that the reason for biological specificity within the AON is that human actions, relative to non-biological movements, have been observed more frequently while executing corresponding actions.

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