

# FROM THE PERCEPTION OF ACTION TO THE UNDERSTANDING OF INTENTION

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Humans have an inherent tendency to infer other people's intentions from their actions. Here we review psychophysical and functional neuroimaging evidence that biological motion is processed as a special category, from which we automatically infer mental states such as intention. The mechanism underlying the attribution of intentions to actions might rely on simulating the observed action and mapping it onto representations of our own intentions. There is accumulating neurophysiological evidence to support a role for action simulation in the brain.

## SIMULATION THEORY

An account by philosophers of mind, which maintains that one represents the mental activities and processes of others by simulation; that is, by generating similar activities and processes in oneself (see REF. 53).

Humans have an inherent ability to understand other people's minds. This process is a component of a 'theory of mind,' a well-researched topic in both developmental psychology and cognitive neuroscience. Theory-of-mind research and theory has mainly been applied to high-level cognitive processing, such as understanding that other people can have different desires and beliefs from one's own<sup>1</sup>. This review will focus on a much lower — although equally important — level of theory of mind: the ability to understand others people's intentions by observing their actions. Indeed, this basic form of theory of mind might be a prerequisite for the higher-level understanding of others' minds.

We start by describing psychophysical and functional imaging studies showing that biological motion is processed as a special category, to which humans from an early age attribute mental states, such as intention. Next, we suggest a mechanism for inferring intentions from observed actions that might depend on the system that labels the consequences of one's own actions as being produced by one's own intentions. This mechanism might be based on simulating the observed action and estimating the actor's intentions on the basis of a representation of one's own intentions, a notion that is reminiscent of SIMULATION THEORY<sup>2,3</sup>. Finally, we review the evidence that simulation and imitation — or overt action simulation — facilitate intentional attribution. In particular, neurophysiological evidence provides

support for the existence of a matching system between perception and action, which is recruited during imitation.

What is special about biological motion?

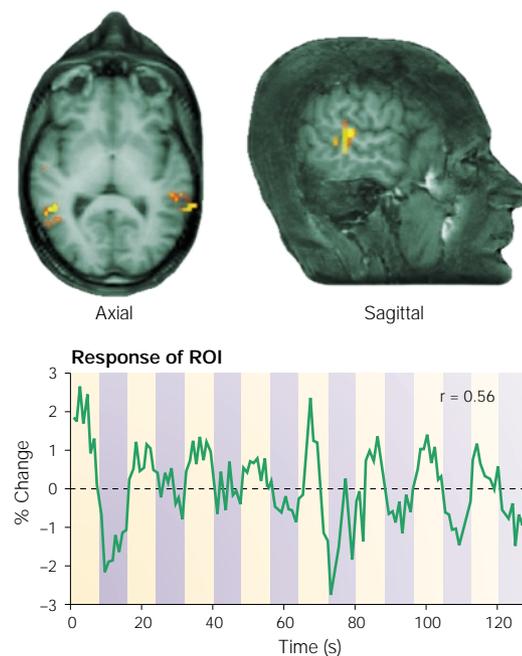
The visual perception of motion is a particularly crucial source of sensory input. It is essential to be able to pick out the motion of biological forms from other types of motion in the natural environment in order to predict the actions of other individuals. An animal's survival depends on its ability to identify the movements of prey, predators and mates, and to predict their future actions, the consequences of which are radically different and could in some cases be fatal. As social animals, humans behave largely on the basis of their interpretations of and predictions about the actions of others.

The Swedish psychologist Johansson<sup>4</sup> devised an ingenious method for studying biological motion without interference from shape. He attached light sources to actors' main joints and recorded their movements in a dark environment. He then showed the moving dot configurations to naive subjects who, rapidly and without any effort, recognized the moving dots as a person walking. Using the same technique, several researchers have shown that observers can recognize not only locomotion, but also the sex of the person, their personality traits and emotions, and complex actions, such as dancing, represented by moving dots<sup>5,6</sup>.

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**Figure 1 | Brain activation in response to biological motion.** The top panel shows axial and sagittal views of the region in the superior temporal sulcus that responds to biological motion. The bottom panel shows the percent of signal change in this region of interest (ROI). A higher level of activity is detected when subjects see biological motion sequences (yellow bars) than when they view scrambled motion sequences (purple bars). Reproduced with permission from REF. 14 © 2001 Elsevier Science.

The perception of biological motion is not restricted to adults<sup>7</sup>. Three-month-old babies can discriminate between displays of moving dots showing a walking person (biological motion) and displays in which the same dots move randomly (non-biological motion)<sup>8</sup>. These studies indicate that the detection of biological motion may become hard-wired in the human brain at an early age. As has been suggested, such a mechanism would be useful in evolutionary terms, and is a classic example of a perception-for-action system<sup>9</sup>, allowing us to recognize the movements of others in order to move towards or away from them.

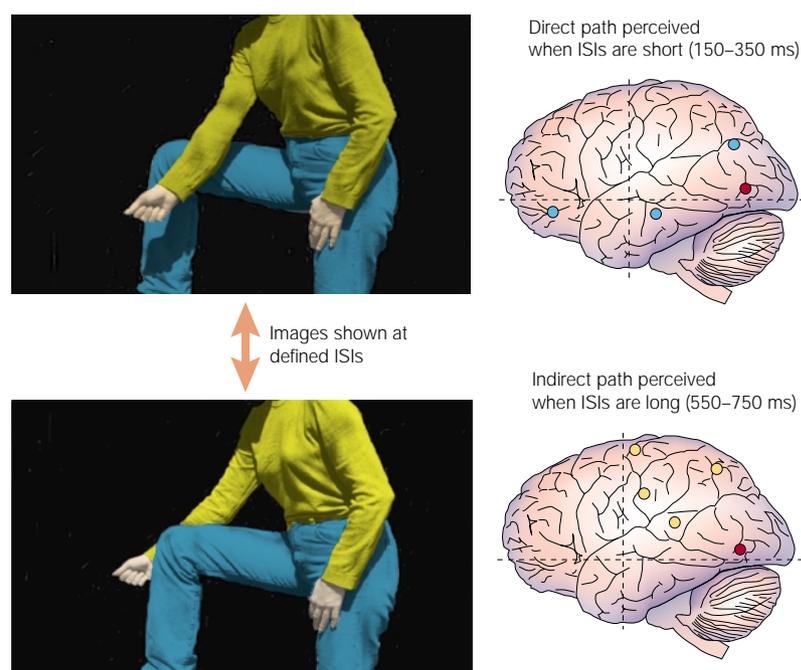
Given the evolutionary importance of detecting biological motion, it is logical to expect specific neural machinery for its perception. Single-cell studies in the monkey superior temporal polysensory area (STP) — which receives input from both the dorsal and ventral visual streams<sup>10</sup> — have identified cells that respond selectively to biological motion<sup>11</sup>. In humans, brain imaging studies have attempted to investigate whether the perception of biological motion is subserved by a specific neural network. One such study used functional magnetic resonance imaging (fMRI) to compare brain regions activated by dot displays showing biological motion, and regions activated by dot displays showing coherent motion, in which all the dots moved at equal velocity in the same direction<sup>12</sup>. The authors found a specific area that was responsive to biological motion, located within the ventral bank of the occipital extent of the

superior temporal sulcus (STS; FIG. 1). This activation was more pronounced in the right hemisphere than in the left hemisphere. A second fMRI study compared dot displays showing biological motion with dot displays showing rigid object motion, in which an object appears to rotate<sup>13</sup>. The responses to rigid motion were localized more posteriorly in the occipito-temporal junction than the responses elicited by biological motion. Activation that was specific to seeing biological motion was detected in the posterior portion of the STS, more prominently in the right hemisphere, and in the left intraparietal cortex. A third fMRI study showed that imagining biological motion activates the same region in the STS<sup>14</sup>. Other neuroimaging studies have detected activation in the right posterior STS in response to seeing hand, eye and mouth movements<sup>15–17</sup>. Clearly, the right posterior STS is important for the detection of biological motion. This area, which is believed to be the human homologue of monkey area STP, receives information from both dorsal and ventral visual streams (involved in vision for action and vision for identification, respectively), rendering it an interface between perception for identification and perception for action<sup>9</sup>. This combination of visual information would be useful for recognizing the movements of other animate beings and categorizing them as threatening or enticing, to predict their future actions and make an appropriate response.

#### Static images convey dynamics

The brain seems to be hard-wired to perceive motion, even in stationary stimuli. Freyd<sup>18</sup> conducted a series of studies showing that still photographs that capture an object in the process of motion induce a perception of movement. When subjects view static images that convey dynamic information, such as an athlete in the posture of throwing a ball, the brain region that is specialized for processing visual motion — the occipito-temporal junction (the medial temporal visual area, MT/V5, and the medial superior temporal area, MST) — is activated. By contrast, images conveying non-dynamic information, such as a person sitting in an armchair, do not activate this area<sup>20</sup>. In other words, the region specialized for visual motion processing is activated by implied motion from static images. This shows that the brain stores internal representations of dynamic information, which can be used to recall past movements and anticipate future movements, even from very partial visual information.

Visual perception of apparent motion can also result from the sequential presentation of static objects in different spatial locations — a clear perception of motion arises from the rapid display of static frames on film, for example. When presented with sequential static images of an inanimate object in different positions, the object is perceived as moving along the shortest or most direct path, even when such a route would be physically impossible — for example, when it would require one object to pass through another<sup>21</sup>. The visual system, therefore, seems to be biased towards selecting the simplest interpretation of the image when it involves inanimate objects. However, the perception of apparent motion operates differently when the object presented is



**Figure 2 | The effects of apparent motion.** The left panel shows examples of stimuli used to create apparent motion. The two pictures are presented alternately with either a short interstimulus interval (ISI) (150–350 ms) or a long ISI (550–750 ms) to produce the subjective impression of mechanically implausible or plausible biological motion, respectively. When presented with a short ISI, subjects report seeing the arm moving through the knee. By contrast, when presented with a longer ISI, subjects report seeing the arm moving around it. The right panel shows activated clusters superimposed on an MRI image. Both plausible and implausible apparent motion resulted in a significant bilateral increase in activity in the medial temporal visual area (MT/V5; red). Clusters resulting from implausible versus plausible apparent motion — in the medial orbitofrontal cortex, the middle temporal gyrus and the precuneus — are blue. Clusters resulting from plausible versus implausible apparent motion — in the left inferior parietal cortex, the premotor cortex, the superior parietal and the supplementary motor area (SMA) — are yellow. The left inferior parietal cortex, premotor cortex and SMA are selectively recruited when apparent motion is compatible with the motor capability of the observer. Conversely, the activation of the temporal lobe during the perception of biomechanically implausible motion indicates that this type of stimulus is processed as object-like and not as a biological figure. The orbitofrontal cortex activity in this condition may reflect the role of this area in filtering out irrelevant information. Adapted with permission from REF. 24 © 2000 Lippincott Williams & Wilkins Ltd.

a human figure<sup>21</sup>. Shiffrar and Freyd<sup>22,23</sup> have shown that viewing images depicting apparent motion of humans, depending on the time interval between the stimuli, gives rise to the perception of either a direct path (biomechanically implausible) or an indirect path (biomechanically plausible; FIG. 2). This model was adapted by Stevens *et al.*<sup>24</sup> to investigate whether a difference in brain activity accompanies this perceptual difference. Using positron emission tomography (PET), they found neural encoding of apparent motion to be a function of the intrinsic properties of the stimulus presented (object versus human), as well as the kind of human movement path perceived (biomechanically possible versus impossible). Premotor and inferior parietal cortex were involved only in the perception of biomechanically possible motion, indicating that these regions are selectively activated to process actions that conform to the capabilities of the observer (FIG. 2). This is in agreement with the idea that the perception of human movement is constrained by an observer's knowledge of or experience with his or her own movement limitations<sup>25</sup>.

### Inferring intentions from biological motion

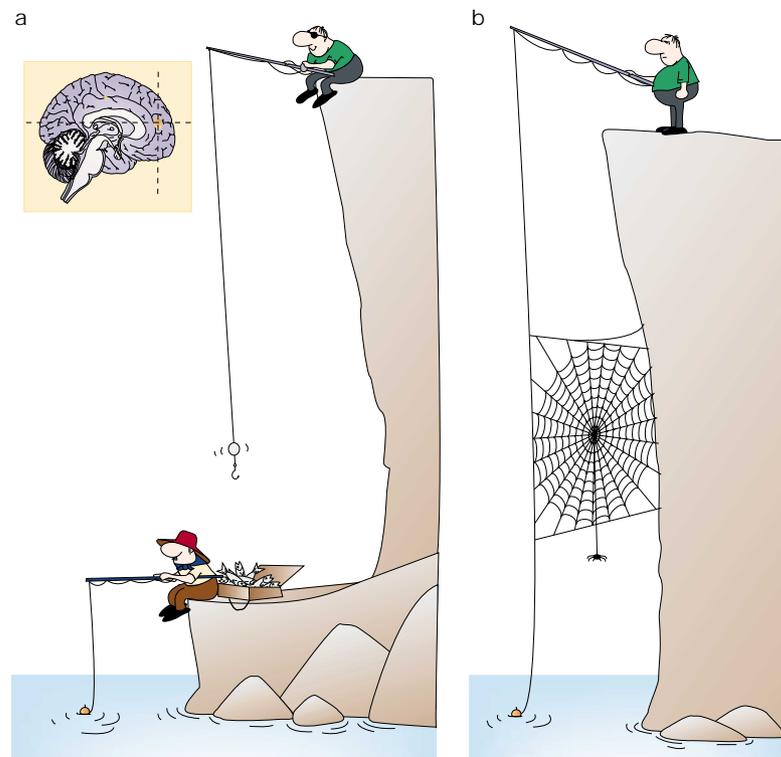
It has been proposed that the detection of biological motion might have evolved to allow us to infer other people's mental states<sup>26</sup>. When we view biological motion, such as Johansson walkers, we attribute mental states such as intentions and desires to the observed movements<sup>6</sup>. For example, when you see someone lifting a glass, you may infer that their intention is to drink from the glass. Humans even infer complex internal states from displays of simple two-dimensional shapes, as long as the movement of the shapes is 'animate' — it is self-propelled, its path may be nonlinear and it may undergo sudden changes of velocity. Heider and Simmel<sup>27</sup> showed that observers who viewed videos of moving triangles could not resist attributing intentions, emotions and personality traits to the shapes. Numerous studies have since demonstrated this automatic attribution of high-level mental states to animate motion in adults<sup>28</sup> in a wide range of cultures (for example, REF. 29), young infants (for example, REF. 30) and even chimpanzees<sup>31</sup>.

Castelli and colleagues<sup>32</sup> used Heider-and-Simmel-like animations in a PET study in which subjects were presented with simple geometrical shapes (triangles), the movement patterns of which evoked either mental-state attribution or simple action descriptions. Their results showed increased activation in association with mental-state attribution in several brain regions, including the medial prefrontal cortex and the temporo-parietal junction (the STS). As described above, the STS is consistently activated by the perception of biological motion. The medial prefrontal cortex is consistently activated by theory-of-mind tasks in which subjects think about their own or others' mental states (BOX 1).

### Recognizing our own intentions

What is the mechanism behind this automatic attribution of intention to other people's actions? Inferring intentions from observed actions might depend on the same mechanism that labels the consequences of one's own actions as being produced by one's own intentions. There is accumulating evidence that we recognize the sensory consequences of our own intentions using a predictive 'forward model' mechanism<sup>33–36</sup>. The forward model automatically predicts the sensory consequences of self-generated intentions and stores the sensory predictions associated with a wide variety of motor actions. Specifically, it is proposed that during self-produced actions the forward model uses efference copy signals<sup>37</sup> that are produced in parallel with the motor command to predict the sensory consequences of the motor act. This sensory prediction is then compared with the actual sensory consequences of the act, and the results of the comparison can be used to determine the source of sensory events<sup>38–40</sup>. Self-produced sensations can be correctly predicted on the basis of efference copy signals. This accurate prediction can be used to cancel or attenuate the ensuing sensation. By contrast, externally generated sensations are not associated with efference copy signals and, therefore, cannot be accurately predicted by the forward model. External

Box 1 | Theory-of-mind tasks



Higher-level theory of mind tasks, such as those involving an understanding of other people's desires and beliefs, have consistently activated the medial frontal lobe (Brodmann area 8/9/32) in functional imaging studies<sup>26</sup>. In the first brain imaging study on theory of mind, subjects were scanned using positron emission tomography (PET) while they performed story comprehension tasks that required the attribution of mental states. In one such story, the subject had to work out that the protagonist's action (a robber giving himself up to the police) was based on his assumption about the policeman's beliefs (that the policeman knew he had robbed a shop). This task required mental-state attribution because the beliefs of the policeman were not made explicit in the story. These theory-of-mind tasks, when compared with comprehension tasks involving 'physical' stories that did not require mental-state attribution, produced activation in the left medial frontal gyrus<sup>71</sup>. The medial frontal gyrus has also been activated in brain imaging studies in which subjects made decisions about the mental states of people depicted in cartoons<sup>72,73</sup> and of 'animate' shapes<sup>32</sup>. The figure shows the medial prefrontal cortex activation during mental-state attribution in a study involving non-verbal stimuli<sup>72</sup>. In this functional magnetic resonance imaging (fMRI) study, healthy subjects were presented with cartoons that either did (left) or did not (right) require mental-state attribution to be understood. The medial frontal gyrus was specifically activated when subjects saw cartoons that involved mental-state attribution compared with those that did not (inset). Reproduced with permission from REF. 72 © 2000 Elsevier Science.

These studies may have implications for the neural bases of **autism** and **schizophrenia**, both of which are characterized by symptoms associated with an impairment in theory-of-mind tasks<sup>74,75</sup>. Indeed, recent studies have shown significantly less activation in the medial frontal gyrus during theory-of-mind tasks in people with Asperger's syndrome — a high-functioning class of **autistic disorder**<sup>76</sup> — and in people with schizophrenia<sup>77</sup>, than in control subjects.

sensations, therefore, cannot be perceptually attenuated. By using such a predictive system, it is possible to cancel or attenuate sensations induced by self-generated movement, and thereby distinguish the sensory consequences of one's own intentions from sensory events arising from an external source.

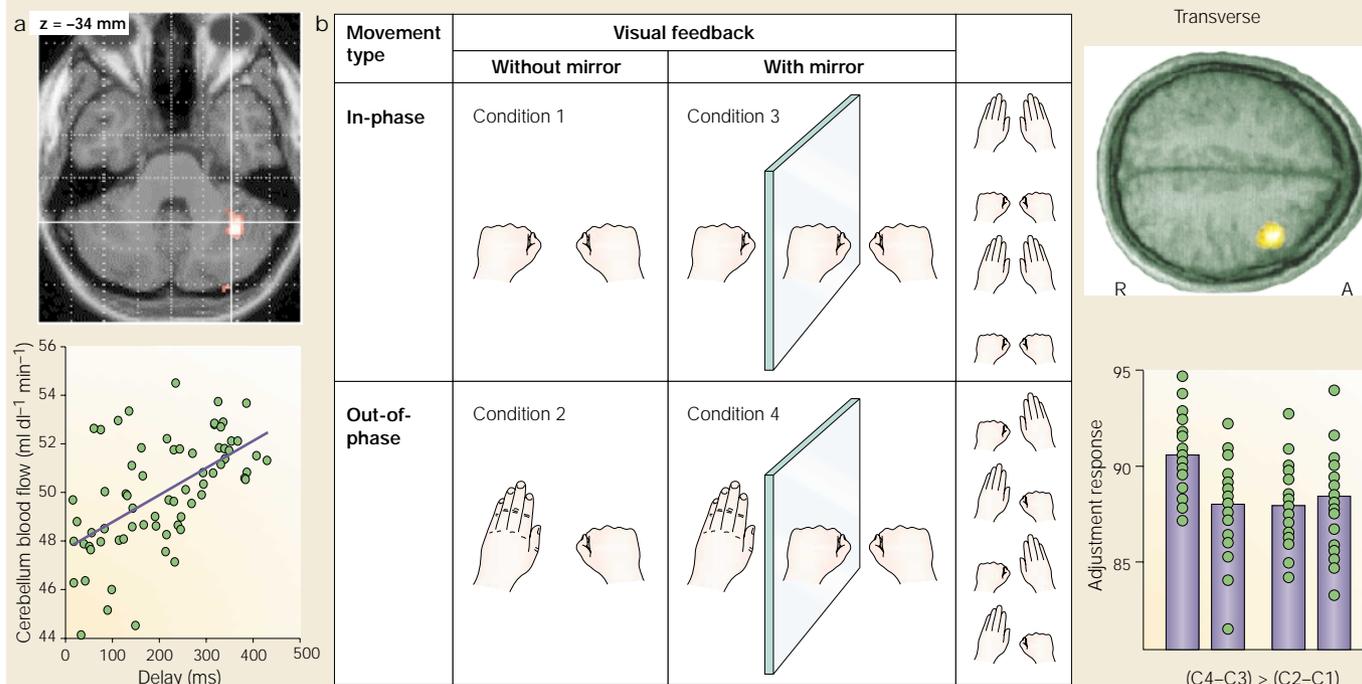
Evidence for this mechanism comes from psychophysical studies that show that subjects experience

external tactile stimulation as more intense than the same stimulation when it is self-produced<sup>41</sup>. The attenuation of self-produced stimulation seems to be mediated, in part, by the 'gating' of neural responses to self-produced stimulation in the brain regions that process that particular modality of stimulus. Somatosensory cortical responses to self-produced touch are attenuated relative to external touch in animals<sup>42–44</sup> and humans<sup>45</sup>. Similarly, auditory cortical responses to self-produced speech are attenuated relative to external speech<sup>46,47</sup>. To be attenuated, self-produced stimuli must be predicted. There is evidence that the cerebellum is involved in such a predictive system, storing representations of motor commands and their sensory consequences, body kinematics, external tools and action contexts, from which predictions are made<sup>45,48–50</sup>. It has been proposed that, together with higher cortical regions, the cerebellum monitors the correspondence between intended and achieved states (BOX 2).

We have briefly described the evidence that motor commands can be used to predict the sensory consequences of self-generated movement, a process that involves the cerebellum. It is possible that the process used by the forward model to predict the sensory consequences of one's own movements could also be used to estimate intentions from the observation of other people's actions. The forward model stores representations of sensory predictions associated with multiple actions<sup>51</sup>. These predictions are based on the motor commands issued to make the actions. This store of predictions of the consequences of self-generated actions could also be used to estimate the motor commands (and therefore the intentions) that gave rise to an action made by another person. The usual direction of prediction in the forward model is from self-generated intentions and motor commands to the consequences of actions. When we observe another person's actions, a related mechanism could operate in the reverse direction. First, the observed sensory consequences (of another person's actions) would be mapped onto stored sensory predictions (of the sensory consequences of one's own actions). These stored representations could then be used to estimate the motor commands and intentions that would normally precede such an action. This could be achieved by automatically and unconsciously simulating the observed action and estimating what our own intentions would be if we produced the same action within the same context.

For example, when thirsty, you might reach for a glass of water with the intention of picking it up and drinking from it. The forward model stores representations of the sensory information associated with these intentions (the weight of the glass, the arm's kinematics and the grip force required to pick up the glass), based on years of experience of picking up glasses. When the brain generates the motor commands to reach and grasp the glass, the forward model predicts the sensory consequences of the motor commands. Now, when you see someone else pick up a glass, the stored representations of the sensory predictions associated with picking up a glass may be recruited and used to estimate what your motor commands and

Box 2 | Monitoring the consequences of an action



There is evidence that the cerebellum is involved in predicting the sensory consequences of motor commands and comparing them with the actual sensory consequences of the movement<sup>33,49,51</sup>. A recent positron emission tomography (PET) study found that regional cerebral blood flow (rCBF) in the cerebellum is correlated with the accuracy of sensory prediction<sup>50</sup>. In this study, subjects used their right hand to move a robotic arm. The motion of this robotic arm determined the position of a second foam-tipped robotic arm, which made contact with the subject's left palm. Using this robotic interface, computer-controlled delays (from 0 to 300 ms) were introduced between the movement of the right hand and its sensory (tactile) consequences on the left. Such a temporal mismatch between movement and its consequences cannot be predicted by the forward model. As the sensory stimulation diverged from the motor command producing it, rCBF in the right cerebellar cortex increased. Panel a shows rCBF in the middle right cerebellar cortex, which correlates with delay between the movement of the right hand and its tactile consequences on the left hand, superimposed on axial slices through a magnetic resonance image (top) and illustrated graphically (bottom; reproduced with permission from REF. 50 © 2001 Lippincott Williams & Wilkins Ltd). In this study, the delays were not detected by the subjects. So, the cerebellum seems to be involved in detecting discrepancies between one's intentions and their consequences at an unconscious, automatic level.

Higher cortical regions, in particular the right dorsolateral prefrontal cortex (DLPFC; Brodmann area 9/46), come in to play when there is a conscious conflict between intentions and their consequences. Fink and colleagues<sup>78</sup> used a mirror device to manipulate the visual feedback that subjects received with their moving arm. In a series of experiments, subjects saw one of their arms and its mirror-reflection, which appeared as if it were their other arm, when opening and closing their fist in synchrony or asynchrony. Panel b (left) shows the four experimental conditions in one of the PET experiments. Subjects made either in-phase or out-of-phase hand-clenching movements, and saw their right hand plus either their real left hand or the reflection of their right hand in the mirror. Condition 4 was the crucial conflict condition, in which subjects received visual feedback of their 'left' hand (actually a reflection of their right hand) when they made out-of-phase movements. The right DLPFC was specifically activated independently of the hand attended when subjects produced asynchronous movements that resulted in a mismatch of visual and sensory feedback (right; R = right, A = anterior; reproduced with permission from REF. 78 © 1999 Oxford University Press). This region is, therefore, activated by a conscious conflict between movement and sensory feedback. When motor intentionality was removed by moving the hands passively — so engendering a mismatch between proprioception and vision only — activation in the right lateral PFC was more ventral (Brodmann area 44/45). The results indicate that the ventral right PFC is primarily activated by discrepancies between signals from sensory systems, whereas the dorsal right PFC is activated when actions must be maintained in the face of a conflict between intention and sensory outcome.

intentions would have been if you had made that same movement. In this way, the forward model could go from the mere observation of someone reaching for a glass, to the estimation that the person's intention is to pick up the glass, lift it to her mouth and quench her thirst.

By simulating another person's actions and mapping them onto stored representations of our own motor commands and their consequences, which are stored in the cerebellum<sup>48,49</sup>, it might be possible to estimate the observed person's internal states, which cannot be read directly from their movements. This simulating system

could also provide information from which predictions about the person's future actions could be made. This is a new framework for an idea reminiscent of the philosophical concept that we understand people's minds by covertly simulating their behaviour<sup>2,3,52,53</sup>. There is accumulating neurophysiological evidence to support a role for action simulation in the brain.

The role of simulation and imitation  
Several cognitive and developmental psychologists have postulated a common coding for actions performed by

the self and by another person<sup>54,55</sup> — also referred to as ‘simulation’<sup>2,3</sup>, ‘resonance behaviour’<sup>56</sup> and ‘shared representations’<sup>57</sup>. In recent years, interest in these concepts has been revived by the neurophysiological discovery of ‘mirror’ neurons in the monkey ventral premotor cortex, which discharge, both when the monkey performs specific goal-directed hand movements and when it observes another individual performing the same movements<sup>58,59</sup>. There is now strong evidence that, in humans, several brain regions, including the premotor cortex, the posterior parietal cortex and the cerebellum, are activated during action generation and while observing and simulating others’ actions. This finding has been made using various neuroimaging techniques, including PET<sup>15,60–62</sup>, transcranial magnetic stimulation (TMS)<sup>63</sup>, fMRI<sup>64</sup> and magnetoencephalogram (MEG)<sup>65</sup>. Particularly interesting is the demonstration that action observation activates the premotor cortex in a somatotopic manner — simply watching mouth, hand and foot movements activates the same functionally specific regions of premotor cortex as performing those movements<sup>66</sup>.

A natural link between action observation and generation is provided by motor imitation. The finding that very young babies can imitate facial gestures indicates an innate, or early developing, system for coupling the perception and production of human actions<sup>67</sup>. Research on neonatal imitation has emphasized its role in non-verbal communication, and indicates that it provides a link between actions and mental states. In an interesting series of experiments<sup>68</sup>, 18-month-old infants were exposed, either to a human, or to a mechanical device attempting to perform various actions (such as pulling apart a dumb-bell), but failing to achieve them. The children tended to imitate and complete the action when it was made by the human, but not when it was made by the mechanical device. This shows that preverbal infants’ understanding of people, but not inanimate objects, is within a framework that includes goals and intentions, which can be gleaned from surface behaviour alone. Meltzoff *et al.* have proposed that imitation might serve as an automatic way of interpreting the behaviours of others in terms of their underlying intentions and desires<sup>69</sup>. This could be achieved if, during imitation, the stored representations of one’s own intentions and the same action contexts were recruited and used to estimate the imitated person’s intentions.

Several functional imaging studies have attempted to explore the neural correlates of imitation in the human brain. In one study, subjects were scanned while they watched actions for later imitation. This resulted in activation in the same parietal and premotor regions that

are involved in producing actions<sup>61</sup>, indicating that, during observation of action, the neural networks subserving motor representations are already tuned for imitation. Importantly, observing actions for later imitation also activated the cerebellum. This would be expected if, during action simulation, the brain recruited the stored representations of one’s own intentions and the same action contexts, which are proposed to be stored in the cerebellum<sup>48,49</sup>. Two recent studies investigated the neural correlates of online imitation. The first, conducted by Iacoboni *et al.*<sup>70</sup> using fMRI, showed increased activation of the parietal lobe, Broca’s area and the somatosensory cortex, during finger movement copying compared with observing finger movements. The second study used PET to explore haemodynamic responses to reciprocal imitation between the observer and experimenter, and found that the right inferior parietal lobule, STS bilaterally, medial prefrontal cortex and cerebellum were specifically activated during imitation compared with matched, non-imitative action (J.D. *et al.*, unpublished observations). The activation of these regions, in particular the STS and medial prefrontal cortex, during imitation lends neurophysiological support to the proposal that motor imitation provides an avenue for developing a theory of mind (BOX 1) — a theory based on evidence of early imitation in infants (for example, see REFS 68,69).

#### Conclusion

The psychophysical and neurophysiological studies that we have reviewed support the idea that the brain is a powerful simulating machine, designed to detect biological motion in order to extract intentions from the motion and to predict the future actions of other animate beings. In the future, it would be interesting to design experiments that directly evaluate unanswered questions regarding the relationship between one’s own intentions and those of others. For example, to what extent, and at what level, is there a real overlap between representations of our own intentions and the intentions of others? How does the brain distinguish between these representations? What is the nature of the mechanisms by which the observation of actions allows us to read intentions? That is, how can the respective contribution of bottom-up and top-down processes in the attribution of intentions to biological motion be disentangled?

#### Links

DATABASE LINKS **Schizophrenia** | **Autistic disorder**  
MIT ENCYCLOPEDIA OF COGNITIVE SCIENCE  
**Theory of Mind** | **Autism** | **Cognitive development**

1. Carruthers, P. & Smith, P. K. (eds) *Theories of Theories of Mind* (Cambridge Univ. Press, Cambridge, UK, 1996).
2. Goldman, A. I. In defense of simulation theory. *Mind Lang.* **7**, 104–119 (1992).
3. Gordon, R. M. In *Theories of Theories of Mind* (eds Carruthers, P. & Smith, P. K.) 11–21 (Cambridge Univ. Press, Cambridge, UK, 1996).
4. Johansson, G. Visual perception of biological motion and a model for its analysis. *Percept. Psychophys.* **14**, 201–211 (1973).
5. Koslowski, L. T. & Cutting, J. E. Recognising the sex of a walker from point-lights mounted on ankles: some second

- thoughts. *Percept. Psychophys.* **23**, 459 (1978).
6. Dittrich, W. H., Troscianko, T., Lea, S. E. & Morgan, D. Perception of emotion from dynamic point-light displays represented in dance. *Perception* **25**, 727–738 (1996).
7. Fox, R. & McDaniel, C. The perception of biological motion by human infants. *Science* **218**, 486–487 (1982).
8. Bertenthal, B. I. in *Visual Perception and Cognition in Infancy* (ed. Granrud, C.) 175–214 (Erlbaum, Hillsdale, New Jersey, 1993).
9. Goodale, M. A. & Milner, A. D. Separate visual pathways for perception and action. *Trends Neurosci.* **15**, 20–25 (1992).

10. Balzer, J., Ungerleider, L. & Desimone, R. Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaque. *J. Neurosci.* **11**, 168–190 (1991).
11. Oram, M. W. & Perrett, D. I. Responses of anterior superior temporal polysensory (STPa) neurons to biological motion stimuli. *J. Cogn. Neurosci.* **6**, 99–116 (1994).
12. Grossman, E. *et al.* Brain areas involved in perception of biological motion. *J. Cogn. Neurosci.* **12**, 711–720 (2000).
13. Grèzes, J. *et al.* Does perception of biological motion rely on specific brain regions? *Neuroimage* **13**, 775–785 (2001).
14. Grossman, E. & Blake, R. Brain activity evoked by inverted and imagined motion. *Vision Res.* **41**, 1475–1482 (2001).

15. Rizzolatti, G. *et al.* Localization of grasp representations in humans by PET. 1. Observation versus execution. *Exp. Brain Res.* **111**, 246–252 (1996).
16. Puce, A., Allison, T., Bentin, S., Gore, J. C. & McCarthy, G. Temporal cortex activation in humans viewing eye and mouth movements. *J. Neurosci.* **18**, 2188–2199 (1998).
17. Wicker, B., Michel, F., Henaff, M. A. & Decety, J. Brain regions associated with mutual gaze: a PET study. *Neuroimage* **8**, 221–227 (1998).
18. Freyd, J. J. in *Attention and Performance XIV: Synergies in Experimental Psychology, Artificial Intelligence, and Cognitive Neuroscience* (eds Meyer, D. & Kornblum, S.) 99–119 (MIT Press, Cambridge, Massachusetts, 1993).
19. Watson, J. D. *et al.* Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb. Cortex* **3**, 79–94 (1993).
20. Kourtzi, Z. & Kanwisher, N. Activation in human MT/MST by static images with implied motion. *J. Cogn. Neurosci.* **12**, 48–55 (2000).
- This fMRI study found greater activation in area MT/MST when viewing static photographs with implied motion than when viewing photographs without implied motion. It is one of the first neurophysiological demonstrations that dynamic information can be extracted from still photographs.**
21. Shiffrar, M. in *Handbook of Perception* (ed. Goldstein, E. B.) 238–263 (Blackwell, Oxford, 2001).
22. Shiffrar, M. & Freyd, J. J. Apparent motion of the human body. *Psychol. Sci.* **1**, 257–264 (1990).
23. Shiffrar, M. & Freyd, J. J. Timing and apparent motion path choice with human body photographs. *Psychol. Sci.* **4**, 379–384 (1993).
- An excellent demonstration of the cognitive mechanisms involved in human motion perception.**
24. Stevens, J. A., Fonlupt, P., Shiffrar, M. A. & Decety, J. New aspects of motion perception: selective neural encoding of apparent human movements. *Neuroreport* **11**, 109–115 (2000).
25. Shiffrar, M. When what meets where. *Curr. Dir. Psychol. Sci.* **3**, 96–100 (1994).
26. Frith, C. D. & Frith, U. Interacting minds — a biological basis. *Science* **286**, 1692–1695 (1999).
- An elegant article that reviews developmental and neuroscientific studies on 'mentalizing,' and proposes that the detection of biological motion may have evolved to enable us to infer other people's mental states.**
27. Heider, F. & Simmel, M. An experimental study of apparent behavior. *Am. J. Psychol.* **57**, 243–249 (1944).
28. Kassir, K. Heider and Simmel revisited: causal attribution and the animated film technique. *Rev. Pers. Soc. Psychol.* **3**, 145–169 (1982).
29. Morris, M. W. & Peng, K. Culture and cause: American and Chinese attributions for social and physical events. *J. Pers. Soc. Psychol.* **67**, 949–971 (1994).
30. Gergely, G., Nadasdy, Z., Csibra, G. & Biro, S. Taking the intentional stance at 12 months of age. *Cognition* **56**, 165–193 (1995).
31. Uller, C. & Nichols, S. Goal attribution in chimpanzees. *Cognition* **76**, B27–34 (2000).
- This fascinating study shows that chimpanzees have an understanding of the 'goals' of two-dimensional objects in simple video displays.**
32. Castelli, F., Happé, F., Frith, U. & Frith, C. D. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement pattern. *Neuroimage* **12**, 314–325 (2000).
33. Ito, M. Neurophysiological aspects of the cerebellar motor control system. *Int. J. Neurol.* **7**, 162–176 (1970).
34. Wolpert, D. M., Ghahramani, Z. & Jordan, M. I. An internal model for sensorimotor integration. *Science* **269**, 1880–1882 (1995).
35. Wolpert, D. M. & Ghahramani, Z. Computational principles of movement neuroscience. *Nature Neurosci.* **3** (suppl.), 1212–1217 (2000).
36. Frith, C. D., Blakemore, S.-J. & Wolpert, D. M. Abnormalities in the awareness and control of action. *Phil. Trans. R. Soc. Lond. B* **355**, 1771–1788 (2000).
37. Von Holst, E. Relations between the central nervous system and the peripheral organs. *Br. J. Anim. Behav.* **2**, 89–94 (1954).
38. Miall, R. C. & Wolpert, D. M. Forward models for physiological motor control. *Neural Netw.* **9**, 1265–1279 (1996).
39. Wolpert, D. M. Computational approaches to motor control. *Trends Cogn. Sci.* **1**, 209–216 (1997).
40. Wolpert, D. M. & Kawato, M. Multiple paired forward and inverse models for motor control. *Neural Netw.* **11**, 1317–1329 (1998).
41. Blakemore, S.-J., Frith, C. D. & Wolpert, D. W. Spatiotemporal prediction modulates the perception of self-produced stimuli. *J. Cogn. Neurosci.* **11**, 551–559 (1999).
42. Jang, W., Chapman, C. E. & Lamarre, Y. Modulation of the cutaneous responsiveness of neurons in the primary somatosensory cortex during conditioned arm movements in the monkey. *Exp. Brain Res.* **84**, 342–354 (1991).
43. Chapman, C. E. & Ageranioti-Belanger, S. A. Comparison of the discharge of primary somatosensory cortical (SI) neurons during active and passive tactile discrimination. *Proc. Third IBRO World Cong. Neurosci.* 317 (1991).
44. Chapman, C. E. Active versus passive touch: factors influencing the transmission of somatosensory signals to primary somatosensory cortex. *Can. J. Physiol. Pharmacol.* **72**, 558–570 (1994).
45. Blakemore, S.-J., Wolpert, D. M. & Frith, C. D. Central cancellation of self-produced tickle sensation. *Nature Neurosci.* **1**, 635–640 (1998).
46. Numminen, J., Salmelin, R. & Hari, R. Subject's own speech reduces reactivity of the human auditory cortex. *Neurosci. Lett.* **265**, 119–122 (1999).
47. Curio, G., Neuiloh, G., Numminen, J., Jousmaki, V. & Hari, R. Speaking modifies voice-evoked activity in the human auditory cortex. *Hum. Brain Mapp.* **9**, 183–191 (2000).
- A magnetoencephalographic study revealing differential responses in human auditory cortex to self-uttered speech compared with listening to a replay of the same speech.**
48. Imamizu, H. *et al.* Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature* **403**, 192–195 (2000).
- An fMRI study in which subjects learned to use a novel tool. The results show that the cerebellum acquires internal models of objects in the external world.**
49. Wolpert, D. M., Miall, R. C. & Kawato, M. Internal models in the cerebellum. *Trends Cogn. Sci.* **2**, 338–347 (1998).
50. Blakemore, S.-J., Frith, C. D. & Wolpert, D. W. The cerebellum is involved in predicting the sensory consequences of action. *Neuroreport* **12**, 1879–1885 (2001).
51. Miall, R. C., Weir, D. J., Wolpert, D. M. & Stein, J. F. Is the cerebellum a Smith predictor? *J. Mot. Behav.* **25**, 203–216 (1993).
52. Hume, D. *Treatise of Human Nature* (Oxford University Press, Oxford, 1978).
53. Gordon, R. M. in *Mind and Morals: Essays on Ethics and Cognitive Science* (eds May, L., Friedman, M. & Clark, A.) 165–180 (MIT Press, Cambridge, Massachusetts, 1996).
54. Meltzoff, A. N. & Moore, M. K. in *Body and the Self* (eds Bermúdez, J., Marcel, A. J. & Eilan, N.) 43–69 (MIT Press, Cambridge, Massachusetts, 1995).
55. Prinz, W. Perception and action planning. *Eur. J. Cogn. Psychol.* **9**, 129–154 (1997).
56. Shepard, R. N. Ecological constraints on internal representations: resonant kinematics of perceiving, imagining, thinking, and dreaming. *Psychol. Rev.* **91**, 417–447 (1984).
57. Barresi, J. & Moore, C. Intentional relations and social understanding. *Behav. Brain Sci.* **19**, 107–154 (1996).
- An interesting cognitive model that attempts to explain how social organisms represent the intentional relations of themselves and other agents.**
58. Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. Action recognition in the premotor cortex. *Brain* **119**, 593–609 (1996).
59. Gallese, V. & Goldman, A. Mirror neurons and the simulation theory of mind reading. *Trends Cogn. Sci.* **2**, 493–501 (1998).
60. Decety, J. *et al.* Mapping motor representations with PET. *Nature* **371**, 600–602 (1994).
61. Decety, J. *et al.* Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* **120**, 1763–1777 (1997).
62. Ruby, P. & Decety, J. Effect of the subjective perspective taking during simulation of action: a PET investigation of agency. *Nature Neurosci.* **4**, 546–550 (2001).
63. Fadiga, L., Fogassi, L., Pavesi, G. & Rizzolatti, G. Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* **73**, 2608–2611 (1995).
- An important demonstration using TMS of increased activity in the motor system during the observation of actions.**
64. Grèzes, J., Costes, N. & Decety, J. Top down effect of the strategy to imitate on the brain areas engaged in perception of biological motion: a PET investigation. *Cogn. Neuropsychol.* **15**, 553–582 (1998).
65. Hari, R. *et al.* Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc. Natl Acad. Sci. USA* **95**, 15061–15065 (1998).
66. Buccino, G. *et al.* Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* **13**, 400–404 (2001).
- An fMRI study that provides the first functional evidence for a somatotopic pattern of activation in the premotor cortex, similar to that of the classical motor cortex homunculus, elicited by the observation of actions made by another individual.**
67. Meltzoff, A. N. & Moore, M. K. Imitation of facial and manual gestures by human neonates. *Science* **198**, 75–78 (1977).
68. Meltzoff, A. N. Understanding the intentions of others: re-enactment of intended acts by 18-month-old children. *Dev. Psychol.* **31**, 838–850 (1995).
69. Gopnik, A. & Meltzoff, A. N. *Words, Thoughts, and Theories* (MIT Press, Cambridge, Massachusetts, 1997).
70. Iacoboni, M. *et al.* Cortical mechanisms of human imitation. *Science* **286**, 2526–2528 (1999).
71. Fletcher, P. C. *et al.* Other minds in the brain: a functional imaging study of 'theory of mind' in story comprehension. *Cognition* **57**, 109–128 (1995).
72. Gallagher, H. L. *et al.* Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia* **38**, 11–21 (2000).
73. Brunet, E., Sarfati, Y., Hardy-Bayle, M. C. & Decety, J. A PET investigation of attribution of intentions to others with a non-verbal task. *Neuroimage* **11**, 157–166 (2000).
74. Baron-Cohen, S., Leslie, A. M. & Frith, U. Does the autistic child have a 'Theory of Mind'? *Cognition* **21**, 37–46 (1985).
75. Corcoran, R., Mercer, G. & Frith, C. D. Schizophrenia, symptomatology and social inference: investigating 'theory of mind' in people with schizophrenia. *Schizophr. Res.* **17**, 5–13 (1995).
76. Happé, F. *et al.* 'Theory of mind' in the brain. Evidence from a PET scan study of Asperger syndrome. *Neuroreport* **8**, 197–201 (1996).
77. Brunet, E., Sarfati, Y., Hardy-Bayle, M. C. & Decety, J. A PET study of the attribution of intentions to others in schizophrenia: comparison with normal subjects on a non-verbal task. *Schizophr. Res.* **49** (suppl.), 174 (2001).
78. Fink, G. R. *et al.* The neural consequences of conflict between intention and the senses. *Brain* **122**, 497–512 (1999).

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