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In this Issue

Understanding ‘*what*’ others do: mirror mechanisms play a crucial role in action perception

Neurophysiological and imaging studies suggest that the inferior frontal cortex (IFC) implements a mechanism that matches perceived actions to one’s motor representation of similar actions (mirror mechanism) and recent lesion studies have also established that IFC is critical for action perception. However, to date causative evidence that action perception requires activation within the same populations of IFC neurons involved in action execution is lacking. In this issue, Cattaneo and colleagues provide the first direct evidence that mirror mechanisms in IFC influence action perception. We discuss the implications of these findings for the understanding of the functional role of mirror mechanisms.

In the last two decades, neuroscientific research has demonstrated that humans (Mukamel *et al.*, 2010), non-human primates (Rizzolatti and Craighero, 2004) and birds (Prather *et al.*, 2008) are equipped with a particular class of multimodal neurons active during action execution and action perception. These ‘mirror neurons’ (MNs) implement a mechanism that matches perceived actions to one’s motor representation of similar actions. Since the discovery of MNs in the early 90s (di Pellegrino *et al.*, 1992), an increasing body of neuroscientific evidence has supported the old notion—going back to Rudolf Hermann Lotze or William James—that action perception is inextricably linked to action execution. This link implies a bi-directional influence such that: (i) action perception affects motor system activity; and (ii) motor system activity affects action perception (Prinz, 1997).

Several studies using neurophysiological and brain imaging techniques have now provided extensive evidence for point 1, showing that the perception of other people performing motor acts modulates the activity of fronto-parietal regions involved in action execution (Rizzolatti and Craighero, 2004; Van Overwalle and Baetens, 2009). These approaches have been fundamental in elucidating the possible mechanisms underlying action perception and in localizing where such mirror mechanisms are implemented in the brain. However, neurophysiological and brain imaging techniques only provide correlational data and cannot establish whether ‘resonant’ activity in fronto-parietal regions is critical for action perception.

Only in the last few years, lesion methods have been applied to test whether the motor system and in particular, the inferior frontal cortex (IFC, including the ventral premotor cortex and the caudal portion of the inferior frontal gyrus), is essential for action perception (point 2). Studies have now shown that brain damage or ‘virtual lesion’ induced by transcranial magnetic stimulation (TMS) to the IFC reduce performance in tasks requiring: (i) to visually discriminate two similar actions (Urgesi *et al.*, 2007; Moro *et al.*, 2008); (ii) to estimate the weight of objects from the observation of lifting actions (Pobric and Hamilton, 2006); (iii) to judge whether a transitive or intransitive gesture has been correctly performed (Pazzaglia *et al.*, 2008b); (iv) to match an observed action with its typical sound (Pazzaglia *et al.*, 2008a); or (v) to order, in a temporal sequence, snapshots depicting different phases of an action (Fazio *et al.*, 2009). The link between these lesion evidence and studies reporting motor system resonance during action observation was provided by the finding that suppression of IFC also disrupts mirror-like activity in the motor system (Avenanti *et al.*, 2007).

Although such lesion studies have established that a brain region, namely the human IFC, which likely contains MNs, is critical for action perception, they still did not directly prove that the same populations of IFC neurons involved in action execution are also critical for action perception. Such demonstration is essential to provide conclusive evidence on the role of MNs in cognition. In this issue, Cattaneo and colleagues provide the first direct evidence that mirror mechanisms in IFC influence action perception.

The authors used a cross-modal motor-visual adaptation paradigm coupled with a TMS-adaptation stimulation protocol. In a first behavioural experiment, they asked a group of healthy participants to perform a number of

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object-directed actions (push or pull) while their limbs were out of view. Then, they were required to categorize static images showing an actor's hand displacing a ball in a congruent or incongruent direction with respect to the previously performed movements. The contact point between hand and ball was varied so to imply a clear pushing or a pulling action or an ambiguous action that could be perceived both as pushing or pulling. The participants' task was to categorize the observed action as pushing or pulling with a forced-choice foot response. Repeated motor performance induced a visual after effect when categorizing action stimuli, in particular when categorizing ambiguous pictures. Repeated pushing execution biased perceptual categorization of ambiguous stimuli towards pulling, while repeated pulling execution biased perceptual categorization towards pushing. Thus, the after effect following motor adaptation was a bias towards the action *opposite* to the one that had been trained. Similarly to typical visual after effects, this cross-modal after effect was short-lasting and tended to dissipate in time. Authors interpreted the after effect as reflecting motor-to-visual adaptation of the same visuo-motor neurons involved in action execution and observation.

They then asked where such action-specific mirror-like mechanisms were located in the brain? A possible candidate was the IFC, since this region is activated during action execution and observation in humans (Van Overwalle and Baetens, 2009) and, notably, previous functional magnetic resonance imaging (fMRI) studies have reported action-specific unimodal visual and motor (Dinstein *et al.*, 2010), and cross-modal adaptation in this region (Kilner *et al.*, 2009). The use of TMS adaptation (Silvanto and Muggleton, 2008) allowed Cattaneo and colleagues to test whether the IFC is the anatomical locus of the population of action-specific visuo-motor neurons responsible for the cross-modal effect. In a second experiment, the authors used the same cross-modal adaptation paradigm and applied single-pulse TMS at the onset of visual stimuli. In keeping with the behavioural experiment, a clear after effect was found during sham TMS (i.e. when no current was induced in the brain). In contrast, when TMS was applied over the IFC, but not over a control area (the primary motor cortex), the after effect was disrupted. What is the most likely mechanism underlying the disruption of cross-modal after effect after IFC stimulation?

Although the physiological bases of TMS adaptation needs to be clarified, its phenomenology is now established and replicated, consisting in a disruption of the perceptual disadvantage of adaptation in processing the adapted feature. The current view is that the effect of TMS depends on the relative activity state of functionally distinct neural populations within the same stimulated region (Silvanto and Muggleton, 2008). After adaptation, TMS of visual or motor areas may induce behavioural facilitation of the features coded by less active (adapted) neural populations (Silvanto and Muggleton, 2008; Cattaneo *et al.*, 2010). This view may be consistent with the study by Cattaneo and colleagues (this issue) where the facilitation of adapted, less active visuo-motor neurons in IFC may have brought to the disruption of the cross-modal after effect. However, since the bias towards the action opposite to the trained one was simply disrupted, not reversed, one cannot definitively conclude that the TMS selectively stimulated the less active neurons. An alternative interpretation of the findings by Cattaneo and colleagues is that TMS may have simply reset the overall activity of IFC neurons, thus suppressing the action representation established during the action execution training. This hypothesis is still consistent with the view that IFC is crucial for the establishment of the cross-modal after effect and for the influence of action execution on action perception.

The results of Cattaneo and colleagues provide the first causative evidence in humans that the IFC contains mirror-like populations of neurons that are recruited in action execution and observation and may directly influence action perception. They leave open, however, two important issues: (i) Which is the specific function of mirror-like mechanisms in action perception? (ii) When are mirror-like mechanisms critical for action perception?

A number of hypotheses have been formed on the function of MNs, and no consensus has yet arisen. Scholars have suggested that they may be involved in action imitation and observational learning (Rizzolatti and Craighero, 2004), in understanding the goal or in predicting the intention of observed actions (Kilner *et al.*, 2007; Rizzolatti and Sinigaglia, 2010), or in anticipating the visual outcome of ongoing observed actions (Wilson and Knoblich, 2005; Urgesi *et al.*, 2010). Each of the above hypotheses put different emphasis on the influence of motor activity on action perception. If mirror-like mechanisms were to serve imitation alone, motor activity should not necessarily influence perception. If they were to serve intention prediction (e.g. why an action has been performed), motor activity might affect mental inference about the action but not necessarily its perceptual analysis. If they serve to understand the goals (the what of an action), motor activity should influence high-level aspects of action perception, including the categorization of an action as a pull or push. If MNs serve to anticipate actions finally, motor activity should exert a direct impact also on lower level sensory components of action perception, possibly by affecting the visual appearance of a body movement as backward or forward. The action perception task used by Cattaneo and colleagues involved the visual discrimination as well as the high-level categorization of the action stimuli. Since no task was used to control for the visual discrimination of other objects or for the low-level discrimination of the sensory aspects of actions, the results cannot determine at which stage of action perception mirror-like mechanisms are critical.

Cattaneo and colleagues did not directly investigate the specific circumstances in which mirror mechanisms critically affect action perception. However, the findings that cross-modal influence is detected when the visual stimuli are ambiguous may suggest that motor resonance is crucial when perceptual information is degraded. This suggestion is in keeping with the view that motor mechanisms are called into play to solve the computational challenges posed by action perception, that is to fill-in missing or ambiguous information and to provide an anticipatory representation of ongoing actions ahead of their realization (Wilson and Knoblich, 2005; Urgesi *et al.*, 2010). Further studies are needed to directly investigate these issues.

There is now evidence suggesting that in humans mirror-like mechanisms may underlie perception of emotion in others (Gallese *et al.*, 2004; Bastiaansen *et al.* 2009) as well as of bodily sensations such as touch or pain (Bufalari *et al.*, 2007; Avenanti *et al.*, 2009; Keysers *et al.*, 2010). Moreover, recent studies suggest that action-related mirror mechanisms may be widespread in sensorimotor regions (Keysers and Gazzola, 2009). We believe that the paradigm used by Cattaneo and colleagues (this issue) has the potential to disclose the functional role of different brain areas and provide new exciting causative evidence that may be fundamental to understand mechanisms underlying social perception.

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