Neural mechanisms subserving the perception of human actions

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Our ability to generate actions and to recognize actions performed by others is the bedrock of our social life. Behavioral evidence suggests that the processes underlying perception and action might share a common representational framework. That is, observers might understand the actions of another individual in terms of the same neural code that they use to produce the same actions themselves. What neurophysiological evidence, if any, supports such a hypothesis? In this article, brain imaging studies addressing this question are reviewed and examined in the light of the functional segregation of the perceptual mechanisms subtending visual recognition and those used for action. We suggest that there are not yet conclusive arguments for a clear neurophysiological substrate supporting a common coding between perception and action.

Humans move around and interact with their environment and these interactions have intention. The visual perception of human movement is therefore a critical cognitive ability because it provides cues that can be used to interpret the intention of the subject under observation. How is this accomplished? From a developmental perspective we know that infants are able to monitor their own body movements proprioceptively and can detect crossmodal equivalents between those movements-as-felt and the movements they see performed by others[1] (e.g. very young babies mimic the facial expressions of their caregivers). There is plenty of evidence that the human visual system is finely attuned to the perception of human movements. For example, a number of early studies, utilizing the point-light technique (see Box 1), revealed that the kinematic pattern of a movement is sufficient for the perception of human movements[2,3].

It may be hypothesized that perception and recognition processes are mediated by the implicit knowledge of production (motor) rules and that these provide the tools for recognizing biological motion. This idea is supported by experiments in the domain of handwriting in which Viviani and Stucchi[4] have shown that the visual perception of a simple geometrical figure is influenced by implicit knowledge of the rules of graphic production. According to the same authors, perception is constrained by motor control, that is, by the implicit knowledge of the movements that can be produced. Several authors have suggested that motor knowledge can be used to anticipate forthcoming sequences of action when perceiving human movements[5]. Additional support for this

linkage between the sensory and motor systems relates to predictability. Indeed, the control of action requires predictive mechanisms (i.e. internal forward models) which in turn require a preselection of relevant sensory information.

A good illustration of this idea in the saccadic system has been provided by Duhamel, Colby and Goldberg[6]. They have shown that the visual activity in the lateral intraparietal cortex can anticipate the retinal consequences of an intended eye movement before the eye has begun to move. Perception thus serves to predict the consequences of action but it might also predict the intentionality of observed behavior. For example, Runeson and Frykholm[7] asked actors to lift a box and to carry it to a table while trying to give the impression that the box actually weighed more than it did. Observers were able to detect the actors' intentions by observing the pattern of movement of an array of lights attached to the joints of the actors, and thus were not deceived about the actual weight of the box. In a series of elegant studies, Shiffrar and Freyd[8] showed that the perceived motion of human limbs (extrapolated by observers who viewed rapidly alternating pictures) tends to respect the biomechanical and the joint constraints of normal human movement. The above empirical findings may be interpreted in favor of a common-coding approach to perception and action whose core contention is that perceived events and planned actions share a common representational domain (see Box 2).

This hypothesis implies that perception and action share, at least in part, a common structural mechanism. But

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Box 1. The point-light technique

In order to study information from motion pattern *per se* without interference from form, Johansson developed the 'point-light' technique, which involved attaching small light sources to the joints (e.g. wrists, knees, ankles, shoulders) of actors (Ref. a; Fig. I). The actors were dressed in black so that only the lights were visible, and were filmed while performing various movements. When exposed to a single still frame from the film, subjects were unable to identify the image as that of a human figure. However, when the film was run and the lights began to move, the subjects correctly identified the point-light patterns as a person performing a particular action (e.g. walking, running, hopping).

Using this paradigm, Kozlowski and Cutting showed that observers can make very precise discriminations when watching point-light displays, including the recognition of the gender of the actors, presumably by using cues such as gait (Ref. b). Even more remarkably, observers can distinguish themselves from other familiar people (Ref. c). However, when the films were presented upside-down, observers do not report seeing a human figure in a different orientation (Ref. d). Dittrich investigated whether the ability to detect natural motion is in part determined by the content of independent categories of the information that physically characterize the event (Ref. e). In this study, locomotory (e.g. walking, going upstairs), instrumental (e.g. hammering, stirring) and social actions (e.g. greeting, boxing) were presented with the point-light technique in a normal situation (light attached to joints), with inter-joint positioning (lights attached between joints) and upside-down. The subjects' verbal responses and recognition times showed that locomotory actions were recognized more accurately and more rapidly than social and instrumental actions. Furthermore, biological motion was recognized much more accurately and rapidly when the light-spot displays were presented in the normal orientation rather than upside-down. Finally, recognition rate was only slightly impaired in the inter-joint condition. These findings lead Dittrich to argue that coding of dynamic phase relation-
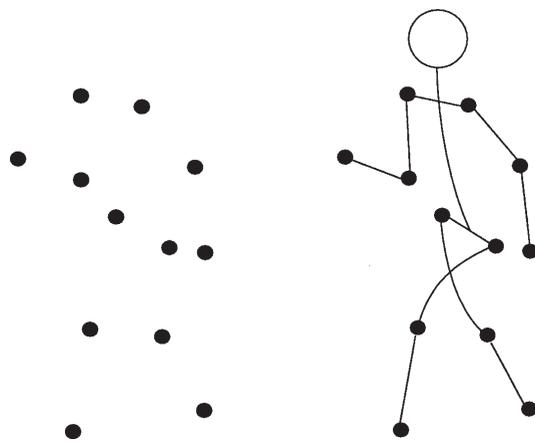
Fig. I. Static illustration of the point-light technique. Lights attached to a person's joints are not perceived as a recognizable object when the person remains stationary in darkness (left). When the person begins to move, the lights are perceived immediately as a human form (right).

ships and semantic coding take place at very early stages of the processing of biological motion.

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is the common-coding model consistent with our knowledge of the functional organization of the visual system? While much of the evidence for the division of labor within the visual system is derived from primate anatomical studies, the broad delineation of two major functional pathways is believed to extend to the organization of the human brain. The ventral pathway projecting from V1 (striate cortex) through areas V2 and V4 (prestriate cortex) to the inferior temporal cortex and to the anterior section of superior temporal sulcus is primarily concerned with the recognition of objects. The dorsal pathway projecting from V1 through areas V2 and V3 to the middle temporal area (V5/MT) and thence to the superior temporal and parietal cortex is concerned with the perception of spatial information and with the visual guidance of actions towards objects[9]. The two pathways are not completely separate; indeed, a polysensory area in the superior temporal cortex receives inputs both from the ventral and dorsal pathways where form and motion can interact[10].

Milner and Goodale[11] substantially reinterpreted these functions on the basis of neuropsychological dissociations in neurological patients. In their model, it is postulated that both streams process information about object features and their spatial localization, but that the visual information is used differentially by each stream (Fig. 1). The ventral pathway is implicated in the recognition, categorization and high-level significance of objects. In contrast, processes supported by the dorsal pathway concern on-line information about the spatial location of objects that is used for the programming and visual control of skilled movements. In this scheme, the primary role of the ventral stream is object recognition whereas the primary role of the dorsal stream is to locate stimuli relative to the observer for the purpose of on-line actions, thus its codes in viewer-centered coordinates. To summarize, the nature of the perception (or action) determines the nature of the processing engaged. This functional dissociation emphasizes the output side of visual analysis rather than the input side.

More recently, Jeannerod[12] has proposed a more general distinction between these two streams that relates to pragmatic and semantic representations of action. The former refers to rapid transformation of sensory input into motor commands, whereas the latter refers to the use of cognitive cues for generating actions. The proposed pragmatic

Box 2. The common-coding model

The common-coding model proposed by Prinz (Ref. a) postulates that perceived events and planned actions share a common representational domain (see Fig. I). The model assumes:

(1) that event codes and action codes are considered as the functional basis of percepts and action plans, respectively;

(2) that they share the same representational domain and are therefore commensurate.

Evidence from induction paradigms (i.e. how certain stimuli induce certain actions by virtue of similarity) and interference paradigms (i.e. mutual interference between the perception of ongoing events and the preparation and control of ongoing action) is found to be compatible with this model (Ref. a).

Related views have been proposed for motion perception (Ref. b) and stimulus–response compatibility (Ref. c).

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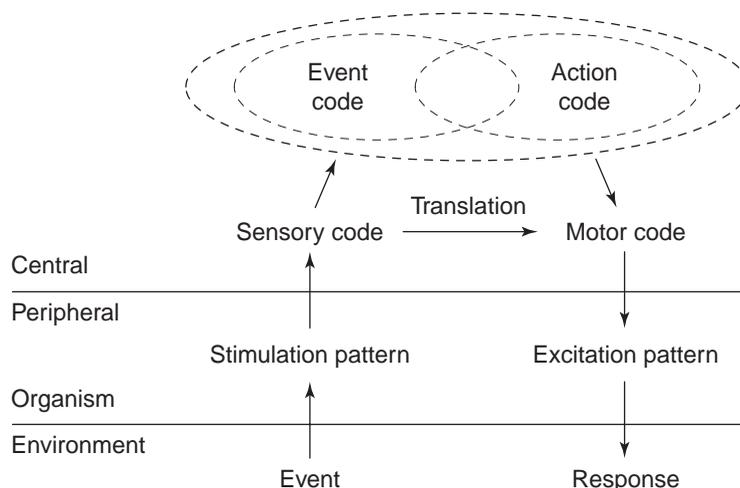
Fig. I. Major functional components that underlie perception and action control. On the left-hand side (upward arrows), events in the environment lead to patterns of stimulation in the sense organs (peripheral) and generate sensory codes in the brain (central). On the right-hand side, the activity travels down, from motor codes to patterns of excitation in the muscles to the action (response). (Adapted from Ref. a, by permission of Psychology Press Limited, Hove, UK.)

representation might depend on cooperation across distributed areas in the parietal lobe and premotor cortex. Neurons in the posterior parietal cortex (area AIP) that discharge in response to the presentation of specific three-dimensional objects and/or during grasping movements directed towards these objects have been described by Taira[13]. This area projects heavily to the ventral premotor cortex, which is characterized by neurons responding to the observation of goal-related hand actions[14]. Thus, according to this view, pragmatic representation involves one of the two visuomotor channels, namely the one operating for grasping (for a recent review see Ref. 15).

What would be the selective involvement, if any, of the two cortical pathways during the perception of human actions? It is reasonable to suppose that the dorsal pathway would be much more engaged when the perceived action has to be reproduced at some later time, as this pathway has a key role in the control of actions, and in pragmatic representation. This would also be consistent with a common-coding model. On the other hand, the ventral pathway might be expected to be more involved when perception has no explicit goal or when perception necessitates a recognition process. When perception is not driven by a specific aim, the respective contributions of the two pathways would be expected to be related to the visual content of the stimuli presented (e.g. real objects, pantomimes, whole body point-lights or hand point-lights). Thus, when the perceived action is object-directed, with the actual object present, then the ventral pathway should be involved. However, what would be the contribution of the ventral pathway when the perceived action does not involve an actual object but merely suggests its presence by means of pantomime, a situation often exploited in testing apraxic patients?

Several neuroimaging studies (PET and fMRI) have recently been performed in the search for neural correlates of perception of human actions, and their results are worth discussing within this framework. One might expect that all studies should report activation of the human area V5 (homologue to monkey V5/MT), which is known to be specifically involved in motion perception. The anatomical position of V5 bears a consistent relationship across species and can be defined as the posterior continuation of the inferior temporal sulcus[16]. Several neuroimaging studies have indeed shown this region to be involved in various experimental situations, provided that the control tasks do not include motion[17–20]. For example, Howard[17] recently used the point-light technique to represent human actions in an fMRI study that compared activity during observation of a man running with observation of random dot motion. Human movement minus random dot motion revealed an area of activation located along the superior border of V5 and activations within both dorsal and ventral divisions of area V3. A bilateral activation was also found in the superior temporal gyrus. This study also demonstrated a specialization for visual motion within the V5 complex. Other types of moving stimuli, such as rotatory motion, were also investigated and produced their own fields of activation that partly overlapped V5. Such specialization might help to explain the rather odd clinical findings of a patient with a lesion confined to V5, who was unable to perceive objects in motion but who could still recognize Johansson-like stimuli (i.e. point-light stimuli)[21–23]. In the monkey brain, cells have been found in the superior temporal polysensory area (STPa) that are selectively responsive to the observation of body movements[24]. It is thus reasonable to suggest that the activation in the superior temporal gyrus found by Howard[17] during the perception of biological movement may correspond to area STPa in the monkey.

Vision for action

Grèzes *et al.*[18], using PET, contrasted the perception of meaningful pantomimes with meaningless movements. Subjects were instructed to observe the actions so that they could imitate them immediately after the scanning session. Activity in both experimental conditions was compared to a baseline condition in which stationary hands were presented. Both meaningful and meaningless actions led to activation in the right cerebellum and in the dorsal pathway extending to the premotor cortex bilaterally (see Fig. 2, Fig. 3A). During observation of meaningful actions, additional bilateral activations were found in the supplementary motor area (SMA) and in the orbitofrontal cortex. The activation of the SMA is consistent with the fact that meaningful actions are internally generated from the subject's repertoire of learned actions, and the SMA is known to participate in the programming and planning of internally triggered behavior[25,26]. The activation located in the orbitofrontal cortex might play a role in the inhibition of motor actions. For example, when a patient with hysterical paralysis was asked to attempt to move her paralysed left leg, her right orbitofrontal cortex was significantly activated[27].

Another way to address the neural mechanisms underlying perception of action is to examine the data from motor imagery studies. Motor imagery exhibits many of the properties of the represented action and its study can be considered as a valid approach for describing the content and the structure of motor representations (see Box 3). Indeed, perception for action engages, to a great extent, a network common to that found during explicit motor imagery[28–31] as well as during implicit motor imagery[32], both of which show activity in cortical areas overlapping those that are activated during the actual performance of motor acts. This is good evidence for a common coding between perception and action if one hypothesizes that when perceiving actions with the aim of imitation, subjects are engaged in an implicit preparation of the movements that are to be reproduced. Such results also provide neurophysiological evidence for the idea, proposed by Vogt[33] based on psychophysical experiments, that the perception–action mediation relies on motor representations that are already activated (or formed) during observation.

Vision for perception

When subjects viewed meaningful and meaningless actions or stationary hands but were not told that they would have to imitate these actions, the perception of hand action, whether meaningful or meaningless, resulted in activation of the same cortical network[18] (see Fig. 3B). This shared network consisted of the superior occipital gyrus and the occipital temporal junction in both hemispheres. The middle temporal gyrus, the lower part of the
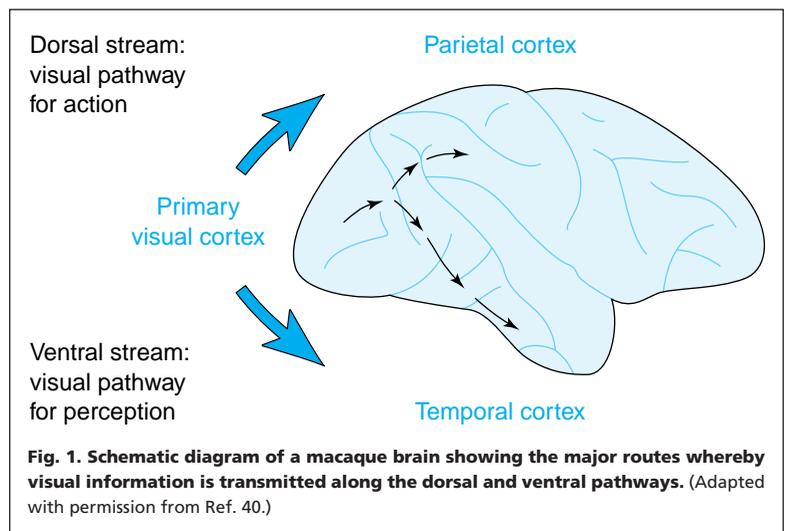
inferior parietal lobe, and the precentral gyrus were also found to be activated within the left hemisphere. The activation of the occipito–temporal junction (BA 19/37) corresponds precisely to the coordinates of V5 given by Watson *et al.*[16]. The site of activation within the precentral gyrus corresponds to the hand representation, indicating that this primary motor region may have been selectively activated by sensory input, an argument that might support a motor theory of perception. In addition to this common network,

Fig. 1. Schematic diagram of a macaque brain showing the major routes whereby visual information is transmitted along the dorsal and ventral pathways. (Adapted with permission from Ref. 40.)
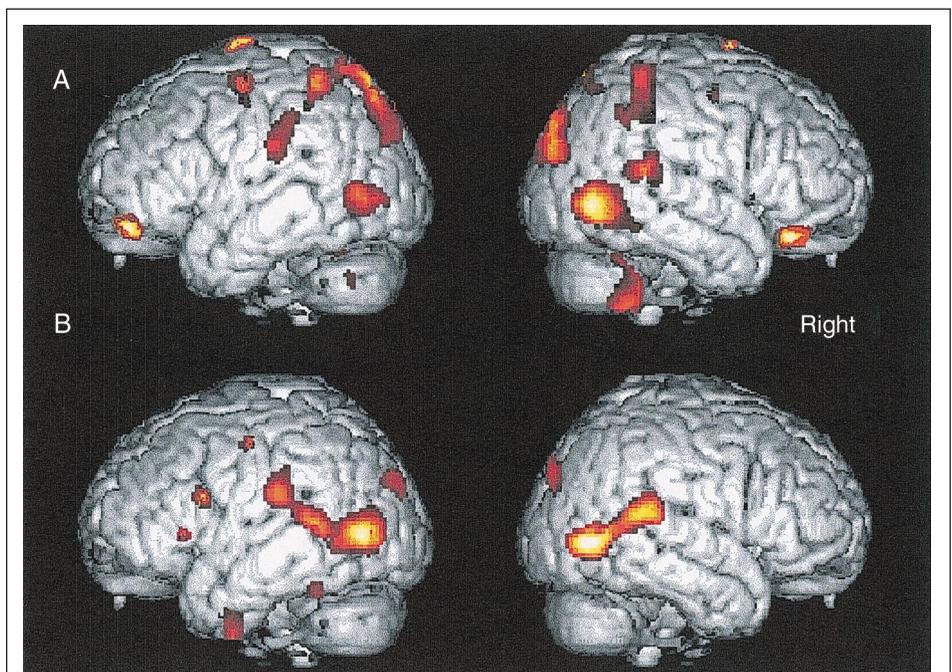
Fig. 2. Localization of significant regional blood flow (rCBF) changes during PET experiments involving perception of meaningful actions. Significant rCBF maps (p<0.001) averaged from 10 healthy volunteers superimposed on an MRI scan centered in Talairach coordinates during the observation of meaningful actions with the intent to reproduce them after the scanning procedure **(A)** and without any specific aim **(B)**. The control condition was observation of stationary hands. Pre-recorded video films comprising sequences of five actions executed by an experimenter with the right upper limb (films showed upper limbs and trunk only) were used as stimuli. Each action, which lasted for 4 s, was separated from the next by a 500 ms blank screen, and was repeated twice in random order (15 stimuli per condition). Different sets of meaningful pantomimes were used in (A) and (B). For the control condition (stationary hands), the stimulus sequence was the same as that used in activation tasks but without movements of the hands. Five spatial positions of the hands and limbs were used and presented randomly throughout the condition. PET data were recorded only during the observation phase. (Adapted from Ref. 18.)

A   Vision for action
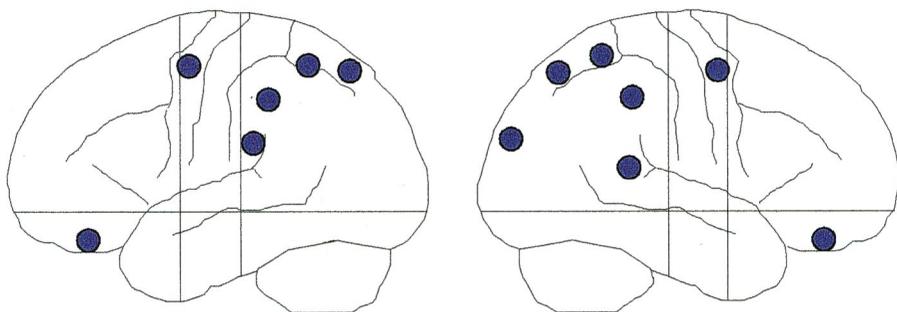
● Observation of meaningful pantomimes to imitate (data from Ref. 18)

B   Vision for perception
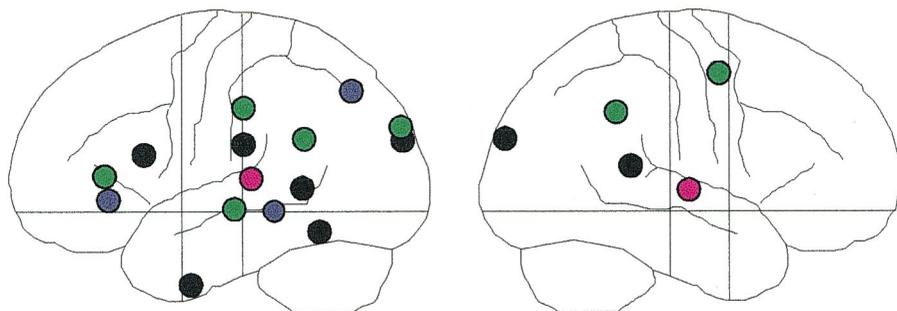
● Observation of grasping real objects (data from Ref. 19)

● Observation of grasping real objects (data from Ref. 35)

● Observation of meaningful pantomimes (data from Ref. 18)

● Observation of biological motion: locomotion (data from Ref. 17)

C   Vision for recognition
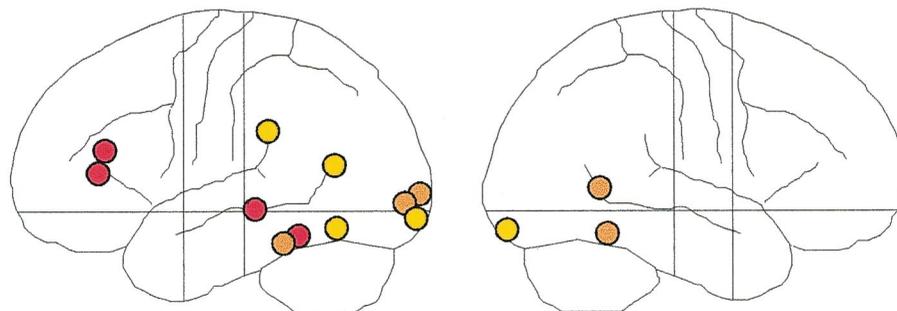
● Observation of biological motion: whole body (data from Ref. 18)

● Observation of biological motion: hand movement (data from Ref. 18)

● Observation of meaningful pantomimes to recognize (data from Ref. 39)

Fig. 3. A summary of the results of neuroimaging studies during perception of action: vision for action (A); vision for perception (B); and vision for recognition (C). Activation foci are shown on a schematic brain registered to Talairach coordinates. For the sake of clarity activations found consistently in the V5 complex are not shown. (Adapted from tables in Refs 17–20,35,36.)

the perception of meaningful actions activated the inferior frontal gyrus, the fusiform gyrus, and the inferior temporal gyrus in the left hemisphere. On the right side, the lingual gyrus was activated. However, meaningless actions engaged the superior parietal lobule in both hemispheres, the inferior parietal lobe in its upper part, and the cerebellum in the right hemisphere. One possibility is that observation of pantomimes activated a neural network in the left hemisphere that might be related to the semantic knowledge of actions, which was decoded from the visual patterns of motion associated with object use (temporal areas and fusiform gyrus). It might also be related to motor commands associated with the use of that object (precentral gyrus). Indeed, the generation of action words activates a similar network in the left hemisphere[34]. In contrast, observation of meaningless movements involved the occipito–parietal pathway bilaterally, which is consistent with the role of the dorsal pathway in processing visual properties of movements and for generating visuomotor transformations.

Additional evidence has been provided by the work of Rizzolatti *et al.*[19] who used PET to study subjects under three experimental conditions: observation of an actor grasping common physical objects, grasping the same objects themselves and, as a control, passive object observation. The results of subtracting object observation from observation of an actor grasping the same object resulted in increased blood flow in the middle temporal gyrus including that of adjacent superior temporal sulcus, in the caudal part of the inferior frontal gyrus, as well as in the precuneus and in the mesial frontal gyrus. All activations were located in the left hemisphere. These results have been confirmed by other PET studies performed by Grafton *et al.*[35] and by Decety *et al.*[36]. According to Gallese *et al.*, the activation in the left temporal lobe might correspond to the STS in monkey and the activation in the pars triangularis might be homologous to area F5 in the ventral premotor cortex of the monkey, in which area the same group has discovered mirror neurons (i.e. neurons that respond both when a particular action is performed and when the same action performed by another individual is observed)[37]. In a recent article, Gallese and Goldman[38] have suggested that the mirror-neuron system in monkey represents the neural correlate of a precursor to a mind-reading ability.

Box 3. Motor imagery

Motor imagery may be defined as a dynamic state during which the representation of a given motor act is internally rehearsed within working memory without any overt motor output. It has been proposed that such a simulation process corresponds to the conscious counterpart of many situations experienced in everyday life, such as watching somebody's action with the desire to imitate it, anticipating the effects of an action, preparing or intending to move, refraining from moving, and remembering an action (Refs a,b). All of these tasks involve motor representations that recruit neural mechanisms specific to action planning. Planning of actions, preparing to move, simulating and observing actions can be regarded as having functional equivalence to the extent that they share these same motor representations and the same neural substrate. The motor representation comprises two parts: a representation of the body as a force-generator, and a representation of the goal of the action encoded in a pragmatic code. The shared neural substrate has been shown by PET and fMRI to include the premotor cortex, supplementary motor area, inferior parietal lobule, cingulate gyrus and cerebellum (Refs c,d).

Several different experimental tasks have been used to address the content of motor imagery in healthy subjects as well as in brain-damaged patients. Results from these experiments showed that the durations of real and mentally performed actions are similar and are governed by central motor rules (for example, Fitts law) (Refs e,f). They also showed that motor imagery activates heart and respiration control mechanisms in proportion to the actual effort that would be required for the real action (Ref. g).

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Perception of meaningful actions engages both ventral and dorsal pathways, mainly in the left hemisphere (Fig. 3B). In all of the above studies, moving hands were presented as either grasping objects or manipulating imagery objects. The fact that the left hemisphere is dominant during perception of actions can be interpreted as the activation of semantic representations related to language[34]. This conclusion is consistent with the left-hemisphere specialization for language and motor control and as attested by the prevalence of apraxia following left hemispheric damage[39].

Vision for recognition

A few PET studies have explicitly addressed the issue of perception of action for the purpose of recognition. The task in these experiments required memory encoding because subjects were aware that they would be given a recognition memory test following the observation phase. Using point-light depictions of goal-directed hand action, Bonda *et al.*[20] instructed their subjects to watch the stimuli in preparation for a subsequent memory test. These authors reported activations in the inferior parietal lobule as well as in the caudal part of the superior temporal sulcus in the left hemisphere (see Fig. 3C).

In a study during which subjects were asked to observe meaningful versus meaningless hand-movement pantomimes for the purpose of later recognition, Decety *et al.*[36] found rCBF increases in the inferior and middle temporal gyri and in the inferior frontal gyrus on the left side, with additional activations in the right parahippocampal gyrus when meaningful actions were observed. Thus vision for recognition appears to rely mainly on the ventral pathway in the left hemisphere, with the exception of a single activation found in the anterior part of the right inferior parietal cortex[20].

Concluding remarks

The distinction between the neural mechanisms mediating vision for the purpose of action and vision for the purpose of perception is primarily grounded in neuropsychological dissociations and the anatomical interconnectivity of the visual areas in the primate cerebral cortex. Recent neuroimaging studies in healthy humans during perception of actions do not fully confirm this separation. When perception has an explicit goal, the data are consistent with the functional segregation of the labor in the visual pathways (see Fig. 3A and 3C). However, when perception has no explicit aim, such as in the studies illustrated in Fig. 3B, both visual pathways are found to be implicated. Thus, the roles of the two pathways are more easily understood when considered from the point of view of the output (top-down processing) as suggested by Milner and Goodale[11,40].

Single-unit studies in the monkey indicate that the neural mechanisms subserving the perception of action are distributed in at least three anatomically distinct cortical areas (temporal, parietal and frontal)[41]. Although the results of imaging investigations with human subjects are in good agreement with monkey data, we still have much to learn before we can bridge the divide between cognitive psychology and neurophysiology. The demonstration of neural

Outstanding questions

- Can a visuomotor somatotopy be demonstrated with neuroimaging during perception of action (for example, is the somatic representation of the left foot activated selectively when one watches a movement involving this part of the body)? This would provide neurophysiological evidence for a common coding between perception and action.
- Is the distinction between transitive actions (object-use) and intransitive actions (e.g. communication) relevant to the question of the functional division of labor within the visual system?
- Would activation studies in neurological patients with focal lesions inform our understanding of the regions involved in the perception of action?
- Could the transient and selective inhibition of motor executive areas (motor, premotor and parietal areas) using transcranial magnetic stimulation during both observation of actions and action recognition provide important evidence with respect to the role and importance of these structures in action perception?

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activation in the systems responsible for action control during the perception of action does not provide conclusive proof of a common-coding model of perception and action. The strong conclusion that the neural substrate for action planning is activated during perception of action holds true only when the goal is to imitate that action. But the neural substrates underlying the action–perception linkage are less clearly defined when the observer has a goal other than imitation in mind. The spatial and temporal limits of current imaging techniques preclude an analysis of the role of subcortical structures. Common coding, as suggested by Prinz[42], might best apply to high-level processing or cognitive levels of representation, that is, to rather late products of perception and rather early antecedents of actions (e.g. the goal and the consequences of a given action). In addition, common coding postulates an amodal representation system, which might be coded in both motor regions and in a distributed network including the prefrontal, parietal and orbitofrontal cortices. It is at this level that the two studies that have reported activation of the premotor cortex during perception of goal-directed movements[18,35] can be interpreted as supporting a common-coding model.

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