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Are cortical motor maps based on body parts or coordinated actions? Implications for embodied semantics

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ABSTRACT

The embodied cognition approach to the study of the mind proposes that higher order mental processes such as concept formation and language are essentially based on perceptual and motor processes. Contrary to the classical approach in cognitive science, in which concepts are viewed as amodal, arbitrary symbols, embodied semantics argues that concepts must be "grounded" in sensorimotor experiences in order to have meaning. In line with this view, neuroimaging studies have shown a roughly somatotopic pattern of activation along cortical motor areas (broadly construed) for the observation of actions involving different body parts, as well as for action-related language comprehension. These findings have been interpreted in terms of a mirror-neuron system, which automatically matches observed and executed actions. However, the somatotopic pattern of activation found in these studies is very coarse, with significant overlap between body parts, and sometimes with multiple representations for the same body part. Furthermore, the localization of the respective activations varies considerably across studies. Based on recent work on the motor cortex in monkeys, we suggest that these discrepancies result from the organization of the primate motor cortex (again, broadly construed), which probably includes maps of the coordinated actions making up the individual's motor repertoire, rather than a single, continuous map of the body. We review neurophysiological and neuroimaging data supporting this hypothesis and discuss ways in which this framework can be used to further test the links between neural mirroring and linguistic processing.

1. Introduction

The theory of embodied semantics states that concepts acquire their meaning by virtue of their association with sensorimotor representations. In other words, the meaning of a concept is represented in the brain by the same neural networks that underlie the perceptual and motor experiences that have been associated with it (Gallese & Lakoff, 2005). This theory departs from the traditional view in cognitive science, which treats concepts as symbolic, amodal entities. Instead, it advances the view that concepts are embodied, multimodal entities, whose neural representations overlap with those of the individual's perceptual and motor experiences. A concept such as *apple*, for instance, would be represented by many of the same cell assemblies that underlie the perception of its reddish color, its round shape, its particular taste, weight, consistency, and so on. Retrieving a concept, thus, would be nothing more than simultaneously reactivating the stored traces of past perceptual and motor experiences associated with it. While in the classical view a concept is regarded as an abstract symbol, having a purely arbitrary association with a person's sensorimotor experiences, the embodied cognition stance sees concepts as "perceptual symbols" – that is, patterns of neural activity in the sensorimotor cortices themselves (Barsalou, 1999).

In the classical symbolic approach, the meaning of a concept is given by its associations, or links, to other, related concepts. In this framework, the retrieval of a particular concept automatically triggers the activation of closely related ones, and its meaning is thus given by the semantic network it activates. However, as Glenberg and Robertson (2000) point out, this view requires a bridge between this semantic network and the objects in the world they refer to. That is, in order to be meaningful, a mental representation (concept) must be somehow mapped onto the real world – or, to be more precise, to our sensorimotor experience of the world. This is sometimes referred to as the "grounding problem". This problem only appears, though, if concepts are thought to exist as a separate form of representation, outside the sensorimotor system. Several authors have proposed, instead, that concepts are represented in the brain by the very sensory and motor neural networks in which they are grounded (Barsalou, Kyle Simmons, Barbey, & Wilson,

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2003; Damasio, 1989; Glenberg, 1997; Lakoff & Johnson, 1999). In the embodied semantics framework there is no "language of thought"; all thought consists essentially of representations derived from actual perceptions of and actions in the world.

Evidence in favor of the theory of embodied semantics has come from a variety of sources, including behavioral, neurophysiologic and neuroimaging studies. Glenberg and his colleagues, for instance, have shown that successful understanding of a sentence requires an assessment of the "affordances" of the objects to which the sentence refers – that is, the ways in which one can interact with these objects in the world, and the ways in which the objects can interact with each other (Borghi, Glenberg, & Kaschak, 2004; Glenberg & Kaschak, 2002; Glenberg & Robertson, 2000). For instance, in order to determine whether a given sentence makes sense, such as "Hang the coat on the upright vacuum cleaner", one needs to derive the necessary affordances for supporting the coat from the concept of vacuum cleaner. Since this sentence conveys a (very likely) novel combination of the concepts involved, such evaluation must rely on one's sensorimotor representations of "vacuum cleaner" and "coat" in order to derive the possible ways in which they can interact. Even though a vacuum cleaner's potential for supporting a coat may have never been part of one's concept of "vacuum cleaner", this potential can be assessed due to the sensorimotor nature of the concept. Likewise, one can easily determine that the sentence "Hang the coat on the upright cup" does not make sense, even though one may have never tried doing that before and failed (Glenberg & Kaschak, 2002).

One corollary of the embodied semantics theory is that action-related concepts, such as reaching, grasping, running, biting, etc. are represented by the same neural networks that underlie the execution of these actions. This hypothesis has been explored in a number of studies, and the evidence has been accumulating in its favor. One interesting piece of evidence suggesting a close connection between the representation of action concepts and the neural control of body movement is the so-called "action-sentence compatibility effect" (Glenberg & Kaschak, 2002). When subjects are asked to decide whether a sentence makes sense, and respond by making manual responses that require movements toward or away from the body, movements in a given direction (e.g., away from the body) are made more difficult when the direction of movement implied by the sentence is in the opposite direction (e.g., *Liz told you the story*).

In a recent study, Glenberg, Sato, and Cattaneo (2008) asked subjects to transfer 600 beans from one container to another, one at a time. The movement of the hand was either toward or away from the body, depending on the location of the target container. Following this procedure, they performed a task in which they had to discriminate sensible from nonsensical sentences. The sentences described transfer of objects (concrete and abstract) toward or away from the reader. They found an interaction between direction of transfer in the sentences and the direction of bean transfer, such that participants were slower in making a decision about sentences describing transfers in the same direction of the performed action. The authors interpreted these results as indicating that transferring the beans induced "short-term plastic changes in the cortical representation of the actions", which affected performance on the semantic discrimination task.

In a related experiment, Scorolli and Borghi (2007) presented subjects with phrases consisting of pairs of nouns and verbs that could, in one condition, refer to mouth or hand actions (e.g., *to suck the sweet* or *to unwrap the sweet*), and, in the other condition, to foot or hand actions (e.g., *to kick the ball* or *to throw the ball*). Participants were asked to decide whether the phrase made sense, and if so, to respond either by saying *yes* to a microphone or by pressing a pedal. They found that responses were faster when the sentences involved actions using the same effector as the response, showing that the motor system was preactivated by the meaning of the sentence in an effector-specific fashion. This result suggests that, in order to understand a sentence that refers to an action involving a specific body part, one must activate the motor circuits that control that body part (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Buccino et al., 2001; Hauk, Johnsrude, & Pulvermüller, 2004; Tettamanti et al., 2005).

If the mere *understanding* of an action concept requires activation of one's own motor plan for that particular action, there must be a neural mechanism for mapping one's perceptions of actions performed by others onto one's respective motor programs, in a relatively automatic way. A candidate neural mechanism has been provided by the discovery of mirror neurons in the monkey brain. Mirror neurons discharge both when the animal executes a particular object-directed action (such as grasping) and when it sees another monkey or a human performing the same action. They are specific to particular categories of actions, such that a mirror neuron tuned to the action of ripping a piece of paper, for example, will not discharge during the execution or observation of a grasping action (Rizzolatti & Craighero, 2004). In other words, mirror neurons discriminate between different categories of actions, but are relatively insensitive to whether the action is being performed by one's own body or by someone else's. Therefore, they offer a neurophysiological basis for the integration of sensory and motor information about actions into multimodal representations. Some mirror neurons in the ventral premotor cortex of the monkey, for instance, increase their firing rate both when the monkey performs a specific hand action, such as cracking a peanut, or when it sees or even hears someone else performing the same action (Kohler et al., 2002). These neurons, thus, seem to represent the monkey's *idea* of the action, rather than any specific motor or sensory component of it. This possibility is further supported by the fact that mirror neurons will not discharge when the action is pantomimed in the absence of the target object, but they will discharge if the monkey sees, for instance, a hand reaching for an object whose view has been occluded by a screen (Umilta et al., 2001). Furthermore, some mirror neurons were found to respond to certain actions regardless of the effector used (e.g. grasping with the hand or grasping with the mouth). These neurons have been dubbed "broadly congruent" mirror neurons, since they seem to encode the goal of the action but not the means by which it is executed. Other neurons respond only when the action (observed or executed) is performed in a particular manner, such as grasping an object with the fingertips, as opposed to the whole hand. These cells are known as "strictly congruent" mirror neurons (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Several lines of evidence suggest a mirror-neuron system exists in humans as well, including functional magnetic resonance imaging (fMRI; Aziz-Zadeh, Iacoboni, Zaidel, & Wilson, 2004; Buccino et al., 2001; Iacoboni et al., 1999), transcranial magnetic stimulation (TMS; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), single cell recordings with depth electrodes (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2007), electroencephalography (EEG; Cochin, Barthelemy, Roux, & Martineau, 1999) and magnetoencephalography (Hari et al., 1998).

Several neuroimaging studies have specifically investigated the representation of action concepts in the human brain (Aziz-Zadeh et al., 2006; Buccino et al., 2001; Hauk et al., 2004; Tettamanti et al., 2005; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004). These studies have shown a selective increase in neural activity in the motor cortex (broadly construed, encompassing both primary motor and premotor cortex, with the latter more often activated in these studies) when subjects observe videos depicting an action, or even when they read or listen to phrases describing actions (Table 1 and Fig. 1). In these studies, activations associated with actions performed with different effectors (e.g. mouth, hand, foot) follow a roughly somatotopic distribution,

Table 1
Stereotactic coordinates of premotor activation peaks for actions executed with the mouth, hand or foot/leg in the five studies that investigated the neural correlates of action concepts. Coordinates in MNI standard space. L = left; R = right; PCG = precentral gyrus; POp = pars opercularis of the inferior frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; IFS = inferior frontal sulcus; SFS = superior frontal sulcus.

Study	Task	Mouth/face	Hand/arm	Foot/leg
Aziz-Zadeh et al. (2006)	Observation	L PCG/POp (-54, 4, 26) R PCG (60, 2, 42)	L PCG/POp (−58, 0, 28) L PCG (−30, −6, 46) R PCG (54, 2, 38)	L PCG/POp (−40, 6, 28) R PCG/POp (50, 12, 26)
Buccino et al. (2001)*	Observation	L PCG (−57, −2, 39) R PCG (48, −2, 35) L POp (−65, 11, 22) R POp (61, 7, 26)	L PCG (−57, −6, 48) R PCG (48, −2, 48) L POp (−65, 3, 26) R POp (57, 12, 14)	L PCG (−32, −12, 69) R PCG (40, −7, 65)
Wheaton et al. (2004)	Observation	R MFG (51, 21, 33)	R PCG (61, −12, 34) R IFS (47, 13, 43)	R SFS (32, 5, 38) L POp (−56, 4, 28) R POp (38, 20, 14)
Hauk et al. (2004)	Language	L POp (−50, 10, 20) R POp (54, 18, 20)	L PCG (−38, −20, 48) L SFG (−22, 2, 64) R MFG (32, −12, 48)	L PCG (−22, −3, 64) L SFG (−8, −26, 64) R SFG (2, 8, 54)
Tettamanti et al. (2005)	Language	L POp (−56, 12, 12)	L PCG (−30, −2, 56)	L SFS (−26, 4, 64)

* Only object-related actions included.

according to the well-known map described by Penfield and Rasmussen (1950). Since these effector-specific activations are usually found in the vicinity of the premotor regions involved in the motor control of the respective effectors, it is possible that they reflect the activity of mirror neurons tuned to specific body parts. Our goal in this paper is to review the neuroimaging studies mentioned above, discussing the possible sources of discrepancies between them in light of a new conceptualization of the organization of motor cortical areas, and exploring the implications of these findings for the structure of the human mirror-neuron system and its role in semantic representations.

2. Somatotopy and the motor cortex

The standard textbook depiction of the functional organization of the human motor cortex, showing an image of the body extended along the length of the precentral gyrus, is derived mainly from the work of Penfield and his associates with neurological patients, employing direct electrical stimulation of the cortex during surgery (Penfield & Rasmussen, 1950). The figure shows a continuous mapping between regions of the precentral gyrus and an upside down image of the whole body, with the feet near the dorsomedial convexity, trunk, neck, arms and hands located along the dorsolateral convexity, and the face and mouth located in the most ventral portion of the gyrus. This somatotopic organization has found some support in recent studies of normal subjects using non-invasive procedures. Brain imaging studies have shown roughly somatotopic activations in the precentral gyrus associated with simple flexion/extension movements of the finger, elbow and feet, and with lateral movements of the tongue (Ehrsson, Geyer, & Naito, 2003; Hauk et al., 2004; Rao et al., 1995). These studies consistently show activations for foot movements localized in the dorsomedial portion of the precentral gyrus and sulcus, with mouth movements activating the most ventral portion of the gyrus, and hand/arm movements activating the dorsolateral region in between the two.

Classically, the motor cortex is conceived as composed by at least two distinct cytoarchitectonic areas: Brodmann area (BA) 4, located in the anterior bank of the central sulcus, and BA 6, occupying the crest of the precentral gyrus and the precentral sulcus. BA 4 has traditionally been thought of as the primary motor cortex (M1), containing a more or less discrete representation of the different body parts, and, supposedly, responsible for implementing the elementary components of more complex actions. BA 6, usually referred to as the premotor cortex (PM), has been thought to contain a somewhat fuzzier map of the body, with more overlap be-

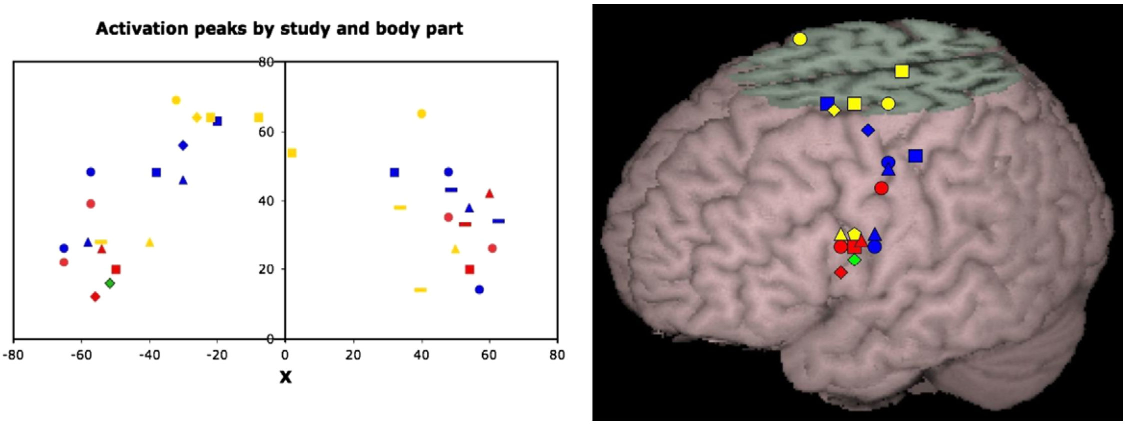

Fig. 1. Location of premotor activation peaks for actions executed with the mouth, hand or foot/leg in the five studies that investigated the neural correlates of action concepts. Left: X and Z MNI coordinates for both hemispheres. Right: projection of activation peaks on the rendered surface of the standard MNI "Colin" brain. Red = face/mouth, blue = hand/arm, yellow = foot/leg, green = conjunction analysis for all three effectors. Triangles, Aziz-Zadeh et al. (2006); circles, Buccino et al. (2001); pentagon/dash, Wheaton et al. (2004); squares, Hauk et al. (2004); rhombuses, Tettamanti et al. (2005).

tween body parts, and encoding more complex action plans. In addition, Brodmann area 44, located in the pars opercularis of the inferior frontal gyrus (POp; adjacent to BA 6), is sometimes referred to as a premotor area, since it has been implicated by several studies in aspects of motor processing (for a review, see Binkofski & Buccino, 2004). However, its particular role in motor control is still largely unknown. Histologically, BA 4 and BA 6 lack an internal granular layer (layer IV), and are thus designated as "agranular". BA 44, on the other hand, contains a layer IV – though poorly defined – and it is therefore referred to as "dysgranular".

In the study by Ehrsson et al. (2003) subjects were asked to imagine themselves performing movements of the mouth, the hand or the foot while in the scanner. The authors were able to localize the activations induced by motor imagery to specific cytoarchitectonic areas by co-registering their data with a population-based map of histologically defined regions. For each of the effectors, both the primary motor cortex (BA 4) and the adjacent premotor cortex (BA 6) were activated in a somatotopic manner.

3. Neuroimaging studies of embodied semantics

According to the theory of embodied semantics, motor areas that are selectively activated during retrieval of a given action-related concept should also be active during execution of that same action. As a consequence, when retrieving a concept involving an action executed with a specific effector – say, the hand – the cortical areas that control execution of hand actions should be activated. One way researchers have investigated this hypothesis is by having subjects passively observe video clips showing actions performed with the hand, the mouth or the foot. In the fMRI study by Buccino et al. (2001), subjects observed object-related actions and non-object-related actions with the mouth (biting or chewing, respectively), hand (grasping or mimicking grasping) or foot/leg (kicking a ball or stepping on a brake pedal). The BOLD signal from each of these conditions was contrasted with the signal recorded while subjects observed static pictures of the corresponding body parts. The dorsolateral region of the precentral gyrus was activated for hand action-videos, while a slightly more dorsal region was activated for foot/leg action-videos, and a more ventral area for videos depicting mouth actions, in agreement with the Penfield map. All conditions produced bilateral activations. Interestingly, frontal areas were activated by observation of both transitive (object-directed) and intransitive (non-object-directed) actions, while inferior parietal areas were activated only by transitive actions. Buccino et al. also found that the more posterior portion of the left IFG (pars opercularis, which roughly corresponds to BA 44) was also activated for transitive hand and mouth actions.

In a related study, Wheaton et al. (2004) presented subjects with video images of non-object-related, meaningless actions of the face, hand and leg (they also used observation of still pictures of the corresponding effectors as the baseline). They found somatotopic, non-overlapping activation clusters in the ventral premotor cortex (PM) for movement of the hand, face and legs, though they were restricted to the right hemisphere. Unexpectedly, observation of the leg action (stepping forward) activated additional bilateral clusters in the inferior frontal gyrus (pars opercularis).

At least one study, however, has found a pattern of somatotopic activations for action observation that cannot be easily explained by the homuncular organization of the motor cortex. In the study by Aziz-Zadeh and colleagues (2006), subjects observed mouth, hand and foot actions, such as a mouth biting a fruit, a hand grasping a fruit, or a foot pressing on a pedal. A group analysis revealed that observation of all actions (relative to rest) produced overlapping activations in the posterior portion of the left inferior frontal gyrus and extending through the left ventral precentral gyrus, with observation of hand actions producing an additional activation cluster in dorsal PM.

A few studies have also investigated whether a somatotopically organized pattern of activation in the PM can be induced by the processing of action-related verbal stimuli. In one such study by Hauk and colleagues (2004), subjects read single action-words or looked at strings of meaningless hash marks (####) while in the scanner. This contrast revealed bilateral activation for action-words in the inferior frontal gyrus (IFG) and the precentral gyrus. Face-related words activated a posterior region of the IFG (pars opercularis), while arm-related words activated clusters in the middle frontal gyrus and the left precentral gyrus. Leg-related words activated dorsal regions of the pre- and post-central gyri in the left hemisphere, as well as the dorsomedial frontal cortex. This pattern, with activation for face action-words located in the ventrolateral aspect of the PM, activation for leg action-words located in dorsomedial PM, and activation for hand action-words in between, suggests that the cortical representation of action concepts follows the same pattern as the representation of the motor plans for action, supporting the embodied semantics theory.

In another fMRI study, Tettamanti and colleagues (2005) contrasted the activation associated with auditorily presented sentences describing concrete actions with that from abstract sentences ("I bite an apple" > "I appreciate sincerity"). Action sentences involved either hand, mouth or leg actions (e.g. grasping, biting, and kicking). A small cluster in the posterior portion of the pars opercularis of left IFG (POp) was activated for all action sentences. The remaining portion of pars opercularis around this region was activated for mouth action-sentences only, extending into superior pars triangularis. The hand area of the precentral gyrus was activated for hand action-sentences only, while the posterior superior frontal sulcus was activated for leg action-sentences only. Again, the dorso-ventral distribution of effector-specific activation clusters along the PM followed a somatotopic organization consistent with the Penfield map.

In the study by Aziz-Zadeh and colleagues (2006), subjects also read phrases describing mouth, hand and foot actions (e.g. *biting the peach*, *grasping the peach*, *pressing the break pedal*). The group analysis revealed that the left IFG and the ventral precentral gyrus were activated for all three categories. Individual-subject analysis showed that the peak voxel from the activation cluster obtained while observing each kind of action was most activated when listening to action phrases that utilized the corresponding effector. In other words, the peak voxel for 'observing hand' was more activated by hand sentences than by sentences related to the mouth or the foot, and so forth. This interaction between action-video category and phrase category was found only in the left hemisphere.

Overall, these results provide strong evidence for the idea that regions of the PM involved in controlling the movements of a particular body part are selectively activated during passive observation of actions performed with that body part, or even during comprehension of words or phrases referring to actions with that same effector. This effector-specific, agent-independent pattern of activations, in turn, may reflect the activity of cells with mirror properties distributed over the whole span of the human PM. If that is indeed the case, the mirror properties of these cells seem to differ from those of the mirror neurons described in the monkey in the rostral portion of the ventral premotor cortex (area F5) and the inferior parietal lobule (area PF/PFG). The monkey mirror neurons respond only to object-directed and communicative actions; they do not respond to observation of mimicked actions or intransitive gestures (Gallese et al., 1996; Rizzolatti & Craighero, 2004). The mirror BOLD activation seen in humans, on the other hand, is found for both transitive and intransitive actions, including simple flexion/extension movements of the fingers, feet and toes. Buccino et al. (2001) reported that observation of transitive actions produced additional activation in the inferior parietal cortex, but transitive and intransitive actions activated the precentral gyrus in much the same way. It is possible, therefore, that the mirror neurons underlying the mirror BOLD activity in PM are tuned not to specific action goals, as are the F5 mirror neurons, but rather to some other dimension of action (this point will be developed in the following sections). It should be noted that the finding of a mirror BOLD activation in the human PM does not necessarily imply the existence of cells with mirror properties, since different neuron populations, in principle, could be responsible for the activations seen during action execution and action observation. To our knowledge, though, such an alternative mechanism has never been proposed in detail, and the activity of neurons that discharge both during execution and observation of actions seems to be the most parsimonious explanation for the mirror BOLD activity.

In sum, the neuroimaging evidence available so far suggests that these premotor regions play a role in the representation of concepts associated with the body parts they control, as predicted by the theory of embodied semantics. This role may be mediated by mirror-like activity of individual neurons, although with different mirror properties than those of F5 mirror neurons.

However, despite the general agreement between the studies reviewed above and the traditional, somatotopic view of the organization of the motor cortex, a closer analysis reveals substantial discrepancies. In the study by Buccino et al. (2001), activations for all three effectors overlapped to some extent in the ventral PM, contrary to what would be predicted by the standard somatotopic map. Also, while Buccino et al. found bilateral activations in the PM for all effectors, Wheaton et al. (2004) found activations for hand and mouth actions only in the right hemisphere. These right hemisphere clusters were also more anterior than those reported by Buccino et al., with the activation peak for the face action located in the middle frontal gyrus, rather than the ventral precentral gyrus. Furthermore, unlike Buccino et al., they found bilateral activation of POp for observation of leg actions, which was located ventrally to the activations for hand and mouth. These results are not easily explained in terms of a purely somatotopic organization of the PM.

There is also substantial variation in the localization of activation peaks between these studies (Aziz-Zadeh et al., 2006; Buccino et al., 2001; Hauk et al., 2004; Tettamanti et al., 2005; Wheaton et al., 2004). Left hemisphere peak coordinates for observation of foot actions, for instance, varied from (−32, −12, 69) in Tettamanti et al. to (−40, 6, 28) in Aziz-Zadeh et al. Activation peaks for action language involving the hand varied from (−50, −10, 36) in Aziz-Zadeh et al. to (−30, −2, 56) in Tettamanti et al. to (−38, −20, 48) in Hauk et al. (all coordinates in MNI space).

We must address some caveats when comparing the location of the activation clusters across these studies. First, although all of the studies discussed above involved a comparison between the processing of actions executed with the upper limbs, lower limbs and mouth, the precise actions and muscle groups involved were not identical. Upper-limb actions involved either the fingers (Hauk et al., 2004; Wheaton et al., 2004), the whole hand (Hauk et al.), or the hand and arm (Aziz-Zadeh et al., 2006; Buccino et al., 2001); mouth actions involved either the tongue (Hauk et al.), the jaw (Wheaton et al.), or the whole mouth (Aziz-Zadeh et al.; Buccino et al.; Hauk et al., Tettamanti et al., 2005); lower-limb actions involved either one foot (Hauk et al.), foot and lower leg (Aziz-Zadeh et al.; Buccino et al.) or both legs and feet (Buccino et al.; Wheaton et al.). In addition, different baselines were used to generate the activation contrasts: still images of the corresponding effectors (Buccino et al.; Wheaton et al.) or rest (Aziz-Zadeh et al.), in the case of action-videos; meaningless hash marks (Hauk et al.), abstract sentences (Tettamanti et al.) or rest (Aziz-Zadeh et al.), in the case of action-related language. Hence, some of the variability in the location of activation peaks might be due to differential involvement of specific body parts.

Another factor that can possibly lead to disparities in BOLD activation peaks is individual variability across subjects. The human brain presents a substantial amount of variability in its cortical morphology, leading to inconsistencies in the relative locations of adjacent anatomical areas across individuals. This could add a confound to neuroimaging studies relying on group analyses. This issue was addressed by Aziz-Zadeh et al. (2006), who performed a subject-by-subject analysis of the activations. The group analysis found no correspondence between activations for action observation of particular effectors and activations for reading sentences describing actions performed with those effectors. For each subject, however, the peak voxel activated by observation of a given effector was reliably most activated by sentences involving that effector. A chart showing the locations of these voxels in stereotactic space indeed reveals a wide distribution of peak activations across subjects for a given effector.

Finally, the primary motor cortex has a much more distinct somatotopic organization than the premotor areas. Therefore, actions performed with different effectors can elicit fMRI activations that are more or less somatotopically organized, depending on the degree to which the premotor cortex is recruited. The tasks and contrasts employed in the aforementioned studies are likely to vary in the extent of premotor cortex involvement, which may explain some of the variability. We believe this may be particularly true regarding recruitment of the pars opercularis of the IFG, as we discuss later.

4. A role for coordinated actions

In this section we will make the case that, beyond and beside the possible confounding factors just mentioned, some of the discrepancies discussed above have other sources. We propose that at least some of the disparities between these results and the expected somatotopic map, as well as the differences in the localization of the activations across studies, arise from the role of organizational principles other than somatotopy in determining the overall structure of the motor cortex (broadly construed). Other authors have also pointed out that somatotopy may be insufficient as an explanatory factor in the organization of cortical motor maps, particularly Fadiga, Fogassi, Gallese, and Rizzolatti (2000), Schieber (2001), Graziano (2006), and Graziano & Aflalo (2007), based primarily on studies of the monkey brain.

The motor cortex of the monkey has been divided into a number of distinct areas, including the primary motor cortex (area F1), dorsal premotor cortex (divided into areas F2 and F7), ventral premotor cortex (areas F4 and F5), the supplementary and presupplementary motor cortices (areas F3 and F6, respectively), and the cingulate premotor areas (Luppino, Matelli, Camarda, Gallese, & Rizzolatti, 1991; Matelli, Luppino, & Rizzolatti, 1985). The idea of somatotopy has been pivotal in the attempts to characterize the functional organization of these areas, along with the notion of hierarchical control. It has been suggested that the primary motor cortex – containing a somatotopic map of the monkey body analogous to the Penfield map (a “simiusculus”) – exerts direct control over the muscles, and is under the influence of the premotor areas. Premotor areas display their own somatotopic maps (though poorly characterized), and are thought to be involved in higher-level motor processes.

However, recent studies cast doubt on this strictly somatotopic and hierarchical model. A series of studies employing electrical micro-stimulation by Graziano and his colleagues, for instance, provide evidence for the idea that, in addition to a map of the body, the motor cortex contains (a) a map of target locations for the hand in peri-personal space, and (b) a map of the animal’s motor repertoire – that is, clusters of neurons dedicated to similar, coordinated, ethologically relevant actions, sometimes involving more than one effector (Graziano, 2006; Graziano & Aflalo, 2007; Graziano, Taylor, & Moore, 2002). These maps span the entire surface of the motor cortex, including primary motor and premotor areas. Their data suggests a map of hand locations around the body in terms of upper/lower body, in terms of close to/far from the body along the line of sight, and in terms of lateral/central space. Stimulation of more dorsal areas, for instance, induce hand movements toward the lower peri-personal space, while stimulation of more ventral sites results in hand movements toward progressively higher locations in space. The ventral premotor cortex also seems to represent hand locations closer to the body along the line of sight, while the rostral portion of the dorsal premotor cortex represents locations farther from the body. The map of the monkey's motor repertoire includes actions such as reaching for an object (dorsal premotor cortex), manipulating an object in the space in front of the chest (ventral primary motor/caudal ventral premotor), bringing something to the mouth (rostral ventral premotor), defending the body against an impending object (ventral premotor/caudal dorsal premotor), and climbing/leaping (supplementary motor cortex). The functional organization of the motor cortex, then, seems to be a compromise between a body map, a hand-location map, and a map of coordinated, ethologically relevant actions.

But how could all of these parameters be simultaneously represented in the two-dimensional cortical sheet? Graziano and Aflalo (2007) propose that the motor cortex contains a number of distorted, discontinuous, overlapping maps that represent each of these organizing factors in a way that maximizes nearest-neighbor relationships, given the requirement that they all must share the same two-dimensional surface. They invoked the concept of Kohonen networks to explain how this combined map can arise. A Kohonen network is an algorithm that allows a neural network to self-organize so as to maximize the representational efficiency of features for which there is no receptive surface. Mapping a two-dimensional receptive surface, such as the retina, onto the visual cortex, for instance, is conceptually trivial, since it requires only topographically organized projections between the two, such that neighboring points on the retina are mapped onto neighboring points on the cortex. Likewise, different regions of the body can be mapped onto the somatosensory cortex by means of topographically organized projections, such that neighboring body parts are represented by neighboring regions of the cortex. But mapping multidimensional features such as color, locations in peri-personal space, or conceptual categories, requires input-dependent self-organization. Kohonen (1982) and Kohonen & Hari (1999) showed that this sort of self-organization can happen given three conditions: (a) the input signal is broadcasted to a large number of processing units (either single neurons or clusters of closely connected neurons) in a given region of the cortex; (b) a winner-takes-all pattern of activation, such that the unit reaching the greatest activation in response to the input signal inhibits the other units; and (c) both the winner and the units spatially closest to it become more strongly tuned to the input signal (i.e., the winner cells force their neighbors to become more responsive to the same input). The result of such self-organization is a topographically organized map of the features in question. Some of the consequences of this process are that feature values which occur more often will have larger cortical representations, that the overall map can be fragmented, such that multiple representations of a given feature value appear, and that regions receiving inputs from different sensory modalities will develop common maps for both modalities, such that activation will be modality-independent (Kohonen & Hari, 1999). Additionally, different features (e.g. body parts, action categories, locations in peri-personal space) can develop overlapping maps in the same cortical region. The complex pinwheel organization of the primary visual cortex, for instance, has been explained in terms of a self-organizing map resulting from the interaction between ocular dominance and line orientation (Aflalo & Graziano, 2006). In sum, the Kohonen algorithm solves the problem of representing a space defined by many dimensions into the two-dimensional cortical sheet, such that spatial continuity is maximized for each dimension.

Interestingly, two studies have used the Kohonen algorithm to demonstrate how concepts can be spatially self-organized on a two-dimensional surface based on their usage pattern. Feeding the network with the pattern of co-occurrence of neighboring words in a corpus of written text (e.g., Grimm brothers' tales) resulted in a semantic map, in which words were grouped by syntactic category and semantic similarity (Kohonen & Hari, 1999). One of the semantic features that spontaneously arose in the map's clustering pattern, for example, was a distinction between animate and inanimate nouns, an impressive feature given the unsupervised nature of the network learning.

Aflalo and Graziano (2006) and Graziano and Aflalo (2007) created a neural network model of the entire lateral surface of the monkey motor cortex (encompassing both premotor and primary motor cortex) using the Kohonen algorithm. The initial state of the network followed a strictly somatotopic map: each region of the two-dimensional network represented one specific body part, with no overlaps or discontinuities, such that the network as a whole contained one coherent map of the whole body. They then presented the network with two additional requisites, such that in its final state the network would also encode (a) a representation of hand locations around the body and (b) a representation of a set of coordinated actions habitually executed by the monkey. The network was then allowed to self-organize according to Kohonen's algorithm in order to satisfy these requisites, with the constraint that nearest-neighbor relationships should be preserved as much as possible. In its final state, the model had developed an organization essentially identical to the one drawn from the electrical stimulation studies, supporting the idea that these three factors – namely, body structure, hand location and behavioral repertoire – account for most of the organizational structure of this region of the monkey cortex.

Preliminary evidence for an analogous organization of the human motor cortex comes from neuroimaging studies of action execution, whose results pose challenges to a strictly somatotopic view. Although several studies have shown that imagining or executing simple movements with the tongue, hand or foot produces distinct, somatotopic activations in both M1 and PM (Ehrsson et al., 2003; Rao et al., 1995; Stippich, Ochmann, & Sartor, 2002), other studies have shown that, at a finer scale, there is a significant overlap between body parts. M1 activations for simple movements of the fingers or the wrist, for instance, overlap almost completely (Sanes, Donoghue, Thangaraj, Edelman, & Warach, 1995); likewise, movements of the hand and the elbow also produce largely overlapping clusters (Rao et al., 1995). The study by Sanes et al. makes it clear that the overlap is not an artifact due to insufficient image resolution, since several distinct clusters are associated with each of the fingers, the thumb and the wrist, and their locations are surprisingly similar for all of these effectors. These results are compatible with the idea that effectors that usually work together in an integrated fashion – which is the case for fingers and wrist, and also for hand and elbow, but not for hand and foot or foot and tongue – tend to have overlapping representations in the motor cortex, organized around programs for particular coordinated actions.

The role of habitual, goal-directed actions in the organization of the motor map has been supported by an ingenious study by Rijntjes and colleagues (1999). The authors identified the motor areas associated with movements of the big toe or the index finger by having subjects trace zigzag patterns with each extremity. Toe movement activated the supplementary motor area (SMA), while index finger movement activated dorsolateral PM. Subjects were then asked to trace their signatures with either the index finger or the big toe. The conjunction analysis between "toe sign > toe zigzag" and "finger sign > finger zigzag" showed an effector-independent activation for the signing action in the dorsolateral precentral gyrus, demonstrating that the action of signing one's name with the toe is controlled by the same PM regions that usually control signing with the hand.

Also relevant for this argument is the discovery that the motor cortex shows a high degree of plasticity in response to experience, with reorganization leading to new patterns of connectivity in a matter of hours (Sanes & Donoghue, 2000). This has been established in non-human mammals with intra-cortical electrical stimulation, peripheral nerve lesions, and change in limb configuration. TMS studies in humans have shown that acquisition of new motor skills leads to measurable changes in the limb representation in M1 (Pascual-Leone, Grafman, & Hallett, 1994). This potential of the motor cortex for experience-dependent reorganization supports the view that shared networks for motor control should emerge for effectors that work in a coordinated fashion during frequently executed, coordinated actions.

Therefore, we suggest that the approximate somatotopy found in the neuroimaging studies that investigated the representation of action concepts in the motor cortex reflects the 'body map' component of the combined map found by Graziano and Aflalo (2007); the inconsistencies across these studies and the discrepancies they show with the classic Penfield map reflect the other two components which were not accounted for in the experiments. At this point, the data available does not allow us to compare the merit of our hypothesis relative to the potential confounding factors discussed in the previous section. Only studies specifically designed to test this hypothesis can provide substantial support to it. If this proposal is indeed true, observation of equivalent hand actions performed around the upper, middle or lower portions of the body should reveal a ventral-to-dorsal gradient in the location of the BOLD activations along the premotor cortex. In turn, observing a customary action performed with different effectors (e.g. closing a drawer with the hand or with the knee) should generate partially overlapping activations, and different actions performed with the same effector in the same region of space should produce different activations. This should hold primarily – if not exclusively – for actions that are familiar, goal-directed and easily recognizable – i.e., for actions that belong to the subject's motor repertoire. Similar activation patterns should also arise in the motor cortex during comprehension of sentences describing concrete, familiar actions under these different circumstances.

5. Different roles for pars opercularis (POp) and premotor cortex (PM)?

Taken as a whole, the five fMRI studies reviewed above reveal distinct patterns of activation in PM and POp during action understanding. While activations for foot, hand and mouth actions seem to activate the PM in a roughly somatotopic fashion, POp shows overlapping activations for all three effectors, at least in some circumstances. For action observation, Aziz-Zadeh et al. (2006) found overlapping activations for mouth, hand and foot actions in POp (extending into the ventral precentral gyrus), plus a separate activation in dorsal PM for hand actions. In Buccino et al. (2001), mouth and hand actions produced overlapping activations in POp, in addition to the non-overlapping activations for mouth, hand and foot in the precentral gyrus. Finally, Wheaton et al. (2004) showed activation of POp for the leg action, in addition to the non-overlapping clusters for all three effectors in PM. The same trend can be seen for the comprehension of action-related language: overlapping activity for all effectors in POp was found in the studies by Aziz-Zadeh et al. (2006) and Tettamanti et al. (2005).

These results seem to suggest that POp and PM play distinct roles in action understanding. What could they be? One aspect that seems to distinguish between the experimental conditions that did and did not activate POp is the goal-directedness of the action. Only the object-directed hand and mouth actions in Buccino et al. (2001) activated POp; the non-object-directed actions (such as pantomiming grasping) activated only the precentral gyrus. All action-videos presented by Aziz-Zadeh et al. (2006) were purposeful, object-directed, and they all activated POp. Although POp was also activated by the action sentences in Aziz-Zadeh et al. and by the action-words in Hauk et al. (2004), we must be cautious in interpreting these activations, since these conditions were contrasted with low-level (i.e., non-linguistic) baselines, and therefore the POp activation could be due, in principle, to the processing of linguistic information. This is not the case for Tettamanti et al. (2005), though, in which the baseline consisted of abstract sentences matching the object-directed action sentences in all linguistic aspects. The overlapping activation they found for all actions on POp is strong evidence for an effector-independent role of POp in understanding object-directed actions. It is also interesting to note that, in the Wheaton et al. (2004) study, the leg action was the only one to activate POp. While all three actions in this study were meant to be meaningless, the leg action is the only one suggestive of a meaningful, goal-directed action – walking toward the subject.

It is possible, therefore, that mirror neurons in PM encode more concrete aspects of the action, such as the detailed kinematics and the end postures of the effectors, while neurons in POp encode only higher-level aspects of the observed action, including its perceived goal or intention, regardless of the effector used. Previous studies have shown that observation of facial expressions and hand movements produces a frontal activation cluster encompassing both POp and the adjacent ventral PM, leading to the conclusion that these two areas constitute the frontal node of the human mirror-neuron system (Buccino, Binkofski, & Riggio, 2004; Buccino, Lui, Canessa, & Patteri, 2004; Leslie, Johnson-Frey, & Grafton, 2004). We propose, instead, that the lateral frontal cortex contains at least two relatively distinct populations of mirror neurons, one located primarily in POp and the other in PM. In this framework, POp mirror neurons are effector-independent, encoding abstract representations of the action goals – including the motor affordances of target objects – analogous to the broadly congruent mirror neurons found in the macaque area F5. Premotor mirror neurons, on the other hand, would be more effector-specific, and encode mostly lower-level parameters of the action, such as direction and velocity of movement, as well as the different regions of peri-personal space to where actions can be directed. They would be less sensitive to the overall goals of executed (and observed) actions.

Evidence for the existence of the latter category of mirror neurons comes from two studies that investigated the properties of monkey PM neurons. Tkach, Reimer, and Hatsopoulos (2007) trained monkeys to perform arm movements in order to reach targets that appeared randomly in a horizontal screen in front of the animal. The monkeys did not touch the targets, they simply moved their arms across a two-dimensional plane under the screen, and kinesthetic sensors recorded the arms position and detected when the hand reached the location directly under the target. The monkeys could not see their own arm and hand, as their sight was occluded by the screen, but they could see a cursor that indicated the hand position. There was also an observation phase, in which the monkeys were trained to keep their arm still (without restraint) while they watched the targets appear on the screen and the cursor move toward them, reproducing what the monkeys saw during the execution phase. Single-cell recording from neurons in primary motor cortex and dorsal PM showed that not only these neurons discharged similarly during execution of arm movements and during observation of the targets and cursor, but their firing pattern also encoded information about direction and velocity of movement. In a related study by a different group (Cisek & Kalaska, 2004), monkeys were trained to manipulate a joystick in order to move a cursor toward a location on the screen. The correct location varied from trial to trial, and was cued by a colored ring in the center of the screen, where the cursor was initially located. In the observation condition, the monkeys simply watched the screen, as the cue appeared and the experimenter (unseen) moved the cursor to an either correct or incorrect location. The authors recorded from single cells in the dorsal PM. Most neurons recorded during the action condition showed strong directional tuning (relative to the target location), and the vast majority of these neurons also presented a similar pattern of activation during the observation condition. In sum, these two studies suggest that neurons in dorsal PM (and primary motor cortex) encode lower-level parameters of both executed and observed actions.

It is also interesting to note that, according to Petrides and Pandya (1994) and Rizzolatti and Arbib (1998), POp is the likely human homolog of the monkey area F5, which, so far, is the only premotor area in the monkey shown to harbor broadly congruent mirror neurons (but see Petrides, Cadoret, and Mackey (2005), and Toni, de Lange, Noordzij, and Hagoort (2008), for alternative views about the monkey homologue of POp).

Several lines of evidence suggest a functional dissociation between POp and PM. Anatomically, as mentioned earlier, these two cortical regions generally correspond to different cytoarchitectonic areas, the dysgranular BA 44 and the agranular area 6, respectively. Although the microstructure of BA 44 seems to be intermediary between that of BA 6 and that of the anteriorly adjacent BA 45 (which is granular), histological studies utilizing quantitative, observer-independent methods have shown that BA 44 is much more similar to BA 45 than to BA 6, at least in the left hemisphere. Analyses of neurotransmitter receptor densities also support a functional distinction between the two areas (Amunts & Zilles, 2006).

A number of functional neuroimaging studies on language processing also indicate PM and POp perform distinct computational roles (see Friederici, 2006, for a review). During sentence comprehension, PM activation is modulated by violations of local phrase structures (noun phrase, prepositional phrase, etc.), but not by the complexity of the syntactic operation necessary to understand the sentence. POp shows the opposite pattern. Studies with artificial grammar learning have produced similar results, with POp being activated during violations of hierarchically structured sequences, while PM is activated by violations of local dependencies in sequence fragments that have been learned as fixed templates. Although such dissociation may be specific for syntactic processing, it is reasonable to expect it to have more general implications.

The idea that POp encodes features related to action goals is supported by a series of experiments (reviewed in Gentilucci & Dalla Volta, 2008) showing that mouth and tongue movements are affected by the observation of object-directed and communicative hand actions, but not by meaningless hand actions, and that this interaction seems to depend crucially on the POp. Spectral analysis of speech sounds (phonemes) reveals that the energy is not equally distributed along the frequency spectrum, but it is concentrated on distinct frequency bands, called formants. Vowel sounds, in particular, are mostly defined by the first two formants (the two lowest-frequency energy peaks). The frequency of the first formant (F1) is determined mainly by the height of the tongue in the mouth cavity, while the frequency of the second formant (F2) reflects the horizontal position of the tongue ("frontness/backness"), as well as lip roundness. One study has shown that, when observing communicative hand gestures (ciao, stop, no) while saying the syllable /ba/ on a microphone, the F2 formant is higher than when observing a non-symbolic gesture. The increase in F2 indicates a forward shift of the tongue during pronunciation, which the authors interpret as homologous to the forward movement of the tongue usually seen in the communicative mouth actions of non-human primates (Gentilucci & Dalla Volta, 2008). This finding suggests that the communicative intention detected in the symbolic hand gestures affected the mouth action in a congruent way. Repetitive TMS (rTMS) directed to the left POp abolishes this effect, but not sham TMS or rTMS to the right homologue (Gentilucci, Bernardis, Crisi, & Volta, 2006). Conversely, several studies have shown that execution, imagery or observation of simple, purposeless flexion/extension movements of the fingers and foot, as well as side-to-side movements of the tongue, activate the correspondent areas of M1 and PM, but not POp (e.g., Ehrsson et al., 2003; Stippich et al., 2002).

Several distinct functions have been attributed to POp in different cognitive domains, including processing of phonological information (Bookheimer, 2002), hierarchical relationships between abstract sequence elements (Friederici, 2006; Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006), syntactic unification (Hagoort, 2005), syntactic movement (Ben-Shachar, Palti, & Grodzinsky, 2004) and action understanding (Gallese et al., 1996; Iacoboni et al., 2005). The functional distinction proposed here is not inconsistent with these proposals, since POp is likely to perform different roles in different domains, depending on the large-scale networks in which it participates during the processing of a task, although a detailed discussion of how these functional accounts relate to each other is beyond the scope of this paper.

In sum, anatomical, neurophysiological, and neuroimaging data seem to support a functional distinction between POp and the ventral PM in action recognition, such that POp is more involved in processing action goals, and PM is more engaged in the computation of lower-level movement parameters. This may indicate that, in the course of human brain evolution since the last common ancestor with the macaque monkeys, different parts of the premotor cortex underwent further specialization, such that the rostral portion of the ventral PM became increasingly devoted to more abstract, goal-related parameters of action control. Again, only future studies specifically designed to test this hypothesis can provide strong support or refutation.

6. Conclusion

Neuroimaging studies that have investigated the role of the motor system in representing action-related concepts have shown a roughly somatotopic distribution of activations for actions involving the hand, the foot and the mouth, but have failed to find a clear map of the body in the premotor cortex. We suggest this is in part due to the fact that the functional organization of the PM may be the result of a compromise between a body map, a map of target locations around the body, and a map of coordinated body postures reflecting the end states of habitual actions, sometimes involving more than a single effector. The resulting map is a complex combination of discontinuous, overlapping maps, in which the same body part may be represented more than once, and whose overall topography maintains only a vague resemblance with Penfield's original map. The possibility exists, of course, that other dimensions of action control also compete for representation.

Another possible aspect of motor cortex organization that may explain the pattern of BOLD activation observed in these studies is a functional distinction between POp and PM. The approximate somatotopy found in PM cortex may reflect the activity of low-level, effector-specific mirror-neurons, while the effector-independent activation found in POp may be a consequence of the specialization of this region for higher-level parameters of action representation, such as goals or intentions.

The available neuroimaging evidence, therefore, generally supports the embodied semantics approach, although the complex organization of the human motor cortex imposes limits to the anatomical localization of complex actions. Therefore, studies aimed at investigating the cortical representation of action-related concepts should take into account the additional organizational principles of the motor cortex discussed above. The existence of mirror-neurons tuned to different levels of the motor control hierarchy, as well as the functional differentiation and possible hierarchical relationships between the different parts of the human motor cortex, are issues that remain to be investigated in more detail.

References

Aflalo, T. N., & Graziano, M. S. (2006). Possible origins of the complex topographic organization of motor cortex: Reduction of a multidimensional space onto a two-dimensional array. *Journal of Neuroscience, 26*(23), 6288.

Amunts, K., & Zilles, K. (2006). A multimodal analisys of structure and function in Broca's region. In Y. Grodzinsky & K. Amunts (Eds.), *Broca's region* (pp. 17–30). New York: Oxford.

Aziz-Zadeh, L., Iacoboni, M., Zaidel, E., & Wilson, S. (2004). Left hemisphere motor facilitation in response to manual action sounds. *European Journal of Neuroscience*.

Aziz-Zadeh, L., Wilson, S., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology, 16*(18), 1818–1823.

Barsalou, L. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences, 22*, 577–660.

Barsalou, L., Kyle Simmons, W., Barbey, A., & Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences, 7*(2), 84.

Ben-Shachar, M., Palti, D., & Grodzinsky, Y. (2004). Neural correlates of syntactic movement: Converging evidence from two fMRI experiments. *NeuroImage, 21*(4), 1320–1336.

Binkofski, F., & Buccino, G. (2004). Motor functions of the Broca's region. *Brain and Language, 89*(2), 362–369.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience, 25*(1), 151–188.

Borghi, A. M., Glenberg, A. M., & Kaschak, M. P. (2004). Putting words in perspective. *Memory & Cognition, 32*(6), 863–873.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience, 13*(2), 400–404.

Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and Language, 89*(2), 370–376.

Buccino, G., Lui, F., Canessa, N., & Patteri, I. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of Cognitive Neuroscience*.

Cisek, P., & Kalaska, J. F. (2004). Neural correlates of mental rehearsal in dorsal premotor cortex. *Nature, 431*(7011), 993.

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: Similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience, 11*(5), 1839.

Damasio, A. R. (1989). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition, 33*(1–2), 25.

Ehrsson, H. H., Geyer, S., & Naito, E. (2003). Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of Neurophysiology, 90*(5), 3304–3316.

Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (2000). Visuomotor neurons: Ambiguity of the discharge or 'motor' perception? *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology, 35*(2–3), 165.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*.

Friederici, A. D. (2006). Broca's area and the ventral premotor cortex in language: Functional differentiation and specificity. *Cortex, 42*(4), 472–475.

Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America, 103*(7), 2458–2463.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119*(Pt 2), 593.

Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *PCGN, 22*, 455–479.

Gentilucci, M., Bernardis, P., Crisi, G., & Volta, R. D. (2006). Repetitive transcranial magnetic stimulation of Broca's area affects verbal responses to gesture. *Journal of Cognitive Neuroscience*.

Gentilucci, M., & Dalla Volta, R. (2008). Spoken language and arm gestures are controlled by the same motor control system. *Quarterly Journal of Experimental Psychology (2006), 61*(6), 944–957.

Glenberg, A. M. (1997). What memory is for. *Behavioral and Brain Sciences*.

Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Review*.

Glenberg, A. M., & Robertson, D. A. (2000). Symbol grounding and meaning: A comparison of high-dimensional and embodied theories of meaning. *Journal of Memory and Language, 43*(3), 379.

Glenberg, A. M., Sato, M., & Cattaneo, L. (2008). Use-induced motor plasticity affects the processing of abstract and concrete language. *Current Biology, 18*(7), R290–291.

Graziano, M. (2006). The organization of behavioral repertoire in motor cortex. *Annual Review of Neuroscience, 29*, 105.

Graziano, M., & Aflalo, T. (2007). Mapping behavioral repertoire onto the cortex. *Neuron, 56*(2), 239–251.

Graziano, M., Taylor, C., & Moore, T. (2002). Complex movements evoked by microstimulation of precentral cortex. *Neuron, 34*, 841.

Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences, 9*(9), 416–423.

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America, 95*(25), 15061.

Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron, 41*(2), 301–307.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology, 3*(3), e79.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science, 286*(5449), 2526–2528.

Kohler, E., Keysers, C., Umilta, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science, 297*(5582), 846–848.

Kohonen, T. (1982). Self-organized formation of topologically correct feature maps. *Biological Cybernetics, 43*, 59–69.

Kohonen, T., & Hari, R. (1999). Where the abstract feature maps of the brain might come from. *Trends in Neurosciences, 22*(3), 135–139.

Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh: The embodied mind and its challenge to western thought*. New York: Basic Books.

Leslie, K. R., Johnson-Frey, S., & Grafton, S. T. (2004). Functional imaging of face and hand imitation: Towards a motor theory of empathy. *NeuroImage*.

Luppino, G., Matelli, M., Camarda, R. M., Gallese, V., & Rizzolatti, G. (1991). Multiple representations of body movements in mesial area 6 and the adjacent cingulate cortex: An intracortical microstimulation study in the macaque monkey. *Journal of Comparative Neurology, 311*(4), 463–482.

Matelli, M., Luppino, G., & Rizzolatti, G. (1985). Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. *Behavioural Brain Research, 18*(2), 125–136.

Mukamel, R., Ekstrom, A., Kaplan, J. T., Iacoboni, M., & Fried, I. (2007). *Mirror properties of single cells in human medial frontal cortex*. Paper presented at the program no. 127.4 2007 abstract viewer/itinerary planner. Society for Neuroscience, San Diego.

Pascual-Leone, A., Grafman, J., & Hallett, M. (1994). Modulation of cortical motor output maps during development of implicit and explicit knowledge. *Science, 263*(5151), 1287–1289.

Penfield, W., & Rasmussen, T. (1950). *The cerebral cortex of man: A clinical study of localization of function*. New York.

Petrides, M., Cadoret, G., & Mackey, S. (2005). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature, 435*(7046), 1235.

Petrides, M., & Pandya, D. N. (1994). Comparative cytoarchutectonic analysis of the human and the macaque frontal cortex. In F. Boller & J. Grafman (Eds.). *Handbook of neuropsychology* (Vol. 9, pp. 17–58). Amsterdam: Elsevier.

Rao, S. M., Binder, J. R., Hammeke, T. A., Bandettini, P. A., Bobholz, J. A., Frost, J. A., et al. (1995). Somatotopic mapping of the human primary motor cortex with functional magnetic resonance imaging. *Neurology, 45*(5), 919.

Rijntjes, M., Dettmers, C., Büchel, C., Kiebel, S., Frackowiak, R. S., & Weiller, C. (1999). A blueprint for movement: Functional and anatomical representations in the human motor system. *Journal of Neuroscience, 19*(18), 8043–8048.

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences, 21*(5), 188.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169–192.

Sanes, J. N., & Donoghue, J. P. (2000). Plasticity and primary motor cortex. *Annual Review of Neuroscience, 23*, 393.

Sanes, J. N., Donoghue, J. P., Thangaraj, V., Edelman, R. R., & Warach, S. (1995). Shared neural substrates controlling hand movements in human motor cortex. *Science, 268*(5218), 1775.

Schieber, M. H. (2001). Constraints on somatotopic organization in the primary motor cortex. *Journal of Neurophysiology, 86*(5), 2125–2143.

Scorolli, C., & Borghi, A. M. (2007). Sentence comprehension and action: Effector specific modulation of the motor system. *Brain Research, 1130*(1), 119–124.

Stippich, C., Ochmann, H., & Sartor, K. (2002). Somatotopic mapping of the human primary sensorimotor cortex during motor imagery and motor execution. *Neuroscience Letters, 331*, 50.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience, 17*(2), 273–281.

Tkach, D., Reimer, J., & Hatsopoulos, N. G. (2007). Congruent activity during action and action observation in motor cortex. *Journal of Neuroscience, 27*(48), 13241–13250.

Toni, I., de Lange, F. P., Noordzij, M., & Hagoort, P. (2008). Language beyond action. *Journal De Physiologie, 102*, 71–79.

Umilta, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing. A neurophysiological study. *Neuron, 31*(1), 155.

Wheaton, K. J., Thompson, J. C., Syngeniotis, A., Abbott, D. F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *NeuroImage, 22*(1), 277–288.