

From ‘acting on’ to ‘acting with’: the functional anatomy of object-oriented action schemata

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Abstract: In this chapter it is proposed that object-based actions can be broadly classified into types. In the first, objects are ‘acted on’ without a specific purpose. In the second, an object is ‘acted with’. In this case the grasp reflects the subsequent goal of the subject. Recent evidence from human functional imaging suggests different neural substrates for acting on an object (dorsal parietal cortex) and for acting with an object (inferior parietal cortex). It is argued that conceptual knowledge of tool use and the pragmatics of action rely on the left hemisphere inferior parietal cortex.

Introduction

How we acquire, retrieve and execute motor skills are core questions in neuroscience. Although the computational structure of a well-learned skill remains unknown, enormous progress has been made in defining the functional anatomy of brain systems involved in action representation. In parallel, computational and psychophysical studies have provided theoretical models of how actions might be represented. Underlying these theories is the concept of the action schema. First proposed by Head in 1926, and elaborated by Bartlett in 1932, the schema can be thought of as an abstract memory representation, plan or script for action (Head, 1926; Bartlett, 1932). From a computational perspective, the schema is a command set that has a finite number of parameters that can be modified to meet task demands (Arbib, 1981). The idea of parameter setting has proven indispensable to computational models, and associated psychophysical investigations, of specific motor behaviors (Iberall et al., 1986). The notion of a schema

as a rule, concept or generalization is also used to characterize motor learning (Schmidt, 1975), where it has proven useful for understanding skill learning in different behavioral contexts.

Despite the conceptual utility of this approach, few links between schema theory and the functional neuroanatomy of motor control exist. A noteworthy exception is the characterization of reach-to-grasp (Arbib et al., 1985; Arbib, 1990; Iberall and Arbib, 1990). Here, grasp affordances of the target object and the timing of hand preshaping with respect to limb transport have been shown to be critical components of a larger prehension schema that can be characterized by a limited set of parameters (Jeannerod, 1984). As discussed below, links between computational models of reach-to-grasp and underlying neural mechanisms have been established in non-human primates. A major challenge is to extend schemata to more abstract motor actions, where parameters must be adjusted to fit task demands of greater complexity, such as tools usage. In this chapter, we consider the problem of tool use as a logical extension of reaching-to-grasp (Johnson, 2002). Based on recent work in functional neuroimaging, we propose that hand-object interactions can be understood in terms of two broad classes of schemata that involve dissociable parietofrontal systems: (1) *acting on* objects

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(reaching, grasping and manipulation) is supported by schemata resulting from on-line, sensorimotor transformations; (2) *acting with* objects (tool use) involves separate schemata arising from distributed practice of skilled actions. For instance, we can *act on* an object as when moving a scissors from one place to another on our desk. This involves schemata for transforming sensory information concerning the attributes of the scissors into one of a potentially large set of postures appropriate for achieving the goal of a stable grip for transportation. Of critical importance in selecting the appropriate action are the physical properties of the target object. For instance, we typically select grasps that allow the opposing forces of the fingers to cancel through objects' centers of mass (Goodale et al., 1994). Or, we can *act with* an object as when grasping and manipulating scissors to clip an article from the newspaper. Here too sensorimotor transformations play an indispensable role in controlling the action. However, selection is guided by a schema that consists of parameters for grasping and manipulating the scissors in the precise and over-learned postures necessary to achieve the goal of dexterous clipping. Consequently, for scissors and many other objects, actions generated by application of *acting with* schemata often differ dramatically from those arising from schemes for *acting on*. More precisely, when using objects as tools we often grasp and manipulate them in ways that are not predicted by their physical properties; i.e., with expertise schemata for acting with come to take precedence over the more stimulus-driven acting on schemata. We argue that these broad behavioral distinctions reflect the operation of two functionally and anatomically dissociable parietofrontal systems specialized for computing these respective schemata.

On the one hand, sensorimotor transformations involved in acting on objects occur in bilaterally organized parietofrontal circuits that have been extensively mapped in non-human primates and recently extended to humans. On the other hand, a century of neuropsychological studies and recent functional imaging data suggest that acting with tools is supported by a left-lateralized system involving the inferior parietal lobule (IPL) and medial frontal gyrus. Both the human proclivity for tool and interspecies differences in cortical architecture within the IPL raise the possibility that this later system may be

unique to human beings. We begin with an overview of relevant anatomic pathways defined in the non-human primate and then review recent human functional imaging studies of tool-related actions.

Neuroanatomy of parietofrontal action circuits

Numerous conventions have been used for parceling parietal and premotor areas in non-human primates, and these are being continuously revised and debated as new data become available (Pandya and Seltzer, 1982; Marconi et al., 2001; Rizzolatti and Luppino, 2001). Posterior parietal cortex (PPC) is separated by the intraparietal sulcus (IPs) into superior (SPL) and inferior parietal (IPL) lobules. In the monkey, SPL consists of several areas that have been defined based on their anatomical and/or functional characteristics including: subdivisions of Brodmann's area (BA) 5 (PE, PEa and PEc) mesial BA 7 (7m), PEci, medial intraparietal (MIP) within the IPs and a portion of the ventral intraparietal (VIP) area located on the rostral bank of the fundus of the IPs. The IPL includes: BA 7a, 7b, PFG (a portion of BA 7), the anterior intraparietal (AIP) and lateral intraparietal (LIP) areas within the IPs, and a portion of the ventral intraparietal (VIP) area located in the caudal bank of the IPs.

Areas within the SPL and IPL are directly and reciprocally interconnected with premotor cortex, and also provide indirect input to dorsal premotor areas vis-a-vis prefrontal cortex. Premotor cortex can be grossly divided into dorsal (PMd) and ventral (PMv) regions, which appear not to be densely interconnected (Kurata, 1991). Further, PMd is subdivided into rostral (F7) and caudal (F2) regions, while PMv consists of F4 and F5. Area F2 is reciprocally interconnected with primary motor area (F1), and is also known to project to the spinal cord directly (He et al., 1993; Wise et al., 1997).

Most of the direct visual input to area PMd in the monkey originates in the SPL (Caminiti et al., 1996); however, area PO (V6a) also provides direct visual input to F7. This is relevant to manual actions because PO is the only known visual area that lacks foveal magnification, and its response properties suggest that it may be important for detecting and localizing objects in ambient vision (Wise et al., 1997; Battaglia-Mayer et al., 2001). Area MIP

receives visual input from PO and projects to both F2 and F7. As discussed below, these circuits appear to be specialized for visuomotor transformations for the control of reaching. The portion of area VIP within SPL also projects to F2. It is important to recognize that many areas within the IPL are also connected directly to PMd (Tanne et al., 1995), albeit less densely (Marconi et al., 2001). These areas include VIP, LIP, PFG, 7a and 7b. Somatosensory information concerning limb position is provided to PMd via a circuit interconnecting PEc/PEip-F2 (Matelli et al., 1998). Recent data suggest that cells in PEc are involved in the integration of eye–hand information for coordinated movements (Ferraina et al., 2001). Although not considered part of PM, it is also worth noting that the frontal eye fields (FEF, BA8) receive input from area LIP, a region known to represent coordinate transformations involved in planning and control of eye movements (Andersen et al., 1997).

The rostral portion of the IPL (7b) provides the major source of afferent projections to area PMv (Godschalk et al., 1984a; Kurata, 1991; Luppino et al., 1999). Area PMv contains two functional subdivisions, areas F4 and F5. Area F5 primarily receives input from AIP, and — as detailed below — appears to be concerned with visuomotor transformations involved in grasping. Area F4 is directly interconnected with VIP, and — as elaborated below — this circuit may play a role in constructing representations of the limbs and surrounding peripersonal space (Graziano and Gross, 1998). Anterior IPL (7b) projects to PMv, including the caudal bank of the lower branch of the arcuate sulcus (F5). The middle inferior parietal lobule (areas PFG and PG) projects to the ventral part of area 46 and area 8, while the posterior IPL (7a) is connected with 46v, 46d, and BA8, as well as the anterior PMd (F7) (Petrides and Pandya, 1984).

The SPL and IPL also project to distinct regions of prefrontal cortex, which in turn provide indirect parietal input to PMd (Cavada and Goldman-Rakic, 1989). The IPL projects to dorsolateral prefrontal cortex (Cavada and Goldman-Rakic, 1989), while SPL projects to dorsomedial prefrontal cortex (Petrides and Pandya, 1984). These prefrontal areas then project to dorsal and medial premotor cortex, respectively (Barbas, 1988). Prefrontal inputs

to PMd are more concentrated in F2, and appear to provide an indirect route for visual information from both IPL and SPL (Wise et al., 1997). From a behavioral perspective, the important point is that electrophysiological investigations conducted over the past decade have revealed that several of these parietofrontal circuits are specialized for computing specific sensorimotor transformations that support different object-oriented actions.

Parietofrontal circuits for acting on objects

Dorsal pathways in reaching

Reaching and pointing are actions in which the task goal is usually linked to a specific spatial target. Thus, the underlying action representation, or schema, is relatively rigid with respect to the overall task goal. As long suggested by psychophysical evidence (Jeannerod, 1981), sensorimotor transformations underlying reaching appear to involve parietofrontal circuits that are dissociable from those involved in computing the relatively more flexible schema necessary for grasping (Jeannerod and Decety, 1995). Reaching toward a target involves transforming a representation of objects' extrinsic spatial properties (i.e., location, orientation), and knowledge of the limb's position into a motor plan. Electrophysiological evidence suggests that the visuomotor transformations for reaching are accomplished within a circuit interconnecting MIP and PMd (Johnson et al., 1993; Caminiti et al., 1996; Johnson and Ferraina, 1996). Cells within area MIP appear to represent the intention to move the arm along a specific trajectory in space. Area PMd also receives direct visual (Caminiti et al., 1996) and higher-level proprioceptive (Lacquaniti et al., 1995) input from the SPL. Somatosensory information concerning limb position is provided to PMd via a circuit interconnecting PEc/PEip-F2 (Matelli et al., 1998). Neurons in PMd use this input to compute representations of both the location of visual targets and the direction of intended forelimb movements needed to acquire targets, even under conditions of non-standard mappings (Shen and Alexander, 1997). Furthermore, a sub-population of PMd neurons respond to specific combinations of sensory cues specifying target location and which limb to use during a manual pointing

task (Hoshi and Tanji, 2000). In other words, single PMd units appear to represent specific schemata for specific reaching actions. From the perspective of schema theory, these are highly specific, stimulus-locked action representations that require a distinct mapping of the limb onto target coordinates.

A number of PET studies have identified extensive activation of PMd, IPs and SPL during reaching, pointing and finger tracking movements (Colebatch et al., 1991; Deiber et al., 1991; Grafton et al., 1992; Kertzman et al., 1997). Recent imaging studies with more refined tasks are beginning to identify putative homologues of monkey areas and in particular, area MIP. Three will be described. In the first, subjects performed pointing movements during PET imaging (Desmurget et al., 2001). During each trial subjects made a lateral saccade from a fixation point to a target LED accompanied by a pointing movement, which — due to inertial differences between the limb versus the eyes — began after the saccade was complete. The task was performed without vision of the hand. Unknown to the subjects, targets were moved during peak saccade velocity, when saccadic suppression made subjects transiently blind. Nevertheless, they made appropriate corrective saccades and early, smooth corrections to reaching movements. After subtracting out corrections related to eye movements, a comparison between reaching scans with error correction versus those with stationary targets revealed activation in the contralateral IPs. As shown in Fig. 1, this site is centered on the medial bank of the IPs, but extends into the lateral bank. The site is a putative homologue of monkey MIP, and appears to be involved in on-line correction of the unfolding reaching schema. This interpretation is supported by results of a separate study using the same task. Here, transcranial magnetic stimulation (TMS) disruption of this same intraparietal area, coincident with hand movement onset, completely blocked on-line error correction without dramatically altering reaches to the original target location (Desmurget, *Nat. Neuro.*, 2000). Because the eyes were already centered on the new target location prior to TMS delivery, lack of reach correction was not due to a failure to detect a shift in target location. Rather, it is attributable to tms blocking feedback based revision of an already unfolding motor schema for reaching.

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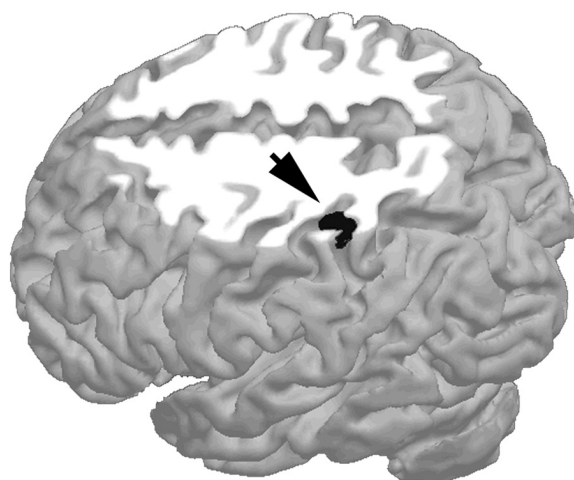


Fig. 1. Putative human homologue of area MIP (defined in non-human primates). The black area (indicated by black arrow) is activated during on-line correction of reaching movements of the contralateral hand (Desmurget et al., 2001). The site is also active during imagined movements when subjects must select the correct hand orientation to grasp an object. In both cases, the activation (Talairach coordinates $-40, -49, 53$) lies on the medial wall of the intraparietal sulcus.

Together, these findings show that this area within the IPs is critical for revising motor schemata in the context of shifting task goal. Specifically the early corrections observed in this task imply that this intraparietal site is involved in computing a dynamic motor error signal for use in updating ongoing reaching actions (see also Prablanc et al., 2003).

In addition to bringing the hand to the target location, reaching for 3-D objects also involves properly orienting the limb to enable appropriate grasping. This depends both on successful integration of sensory information concerning the target object's disposition in space with representations of the effector's biomechanical properties. To investigate areas involved in computation, we developed an event-related fMRI paradigm where subjects plan object-oriented reaching movements without overt execution (Johnson et al., 2000). In this implicit motor imagery paradigm, subjects were required to select whether an under- or overhand posture would be the most comfortable way to grip a handle appearing in a variety of different 3-D orientations. For these choices to be consistent with grip preferences displayed on a comparable task that involved actually grasping

handles, subjects must accurately represent both the stimulus' orientation and biomechanical constraints on pronation and supination of the hand (Johnson, 2000). In contrast to the reaching task described above, these grip selection judgments were made in the absence of overt hand movements and therefore without the benefit of sensory feedback. Nevertheless we reasoned that solving this task should still involve areas that compute schemata for reaching, i.e., a homologue of the MIP-PMd pathway.

Consistent with earlier psychophysical studies (Johnson, 2000), subjects performed these tasks in a manner highly consistent with the biomechanical constraints of the two arms. Grip selection judgments based on either hand induced bilateral activation of PMd in the region of the precentral gyrus. This observation supports the hypothesis that caudal PMd is involved in preparation and selection of conditional motor behavior (Passingham, 1993; Iacoboni et al., 1996; Grafton et al., 1998). In contrast to the bilateral effects observed in PMd, activations within PPC were dependent, in part, on the hand on which grip decisions were based. Left and right hand grip selection each activated regions located within the medial extent of the IPS of the hemisphere contralateral to the involved hand. The site was located less than 5 mm from the area that was activated during on-line correction of reaching movements described above. On the basis of both their locations and functional involvement in reach planning, we believe that this site may be homologous to monkey area MIP. Consistent with this interpretation, responses of cells within area MIP are known to be most pronounced when actions will involve the contralateral hand (Colby and Duhamel, 1991; Colby, 1998). An important point here is that the putative human MIP site was selectively activated by both on-line correction and imagined reaching, the latter of which provided no opportunity for sensory feedback. This suggests that, along with interconnected regions of PMd, the medial IPs is part of a circuit involved in computing motor schemata for both the planning and control of reaching.

Mid-parietal pathways for grasping

In contrast to pointing or reaching to a location in space, the goal of grasping an object can usually

be achieved in numerous ways. Regardless of the final posture, grasping involves transforming intrinsic properties of an object (e.g., shape, size, texture) into a specific configuration of the hand and fingers. In the monkey, this transformation is accomplished in a more ventral circuit connecting areas AIP and F5. Area AIP is part of the IPL and contains several sub-populations of 'manipulation' cells that represent specific types of hand postures necessary for grasping objects (Taira et al., 1990; Sakata et al., 1995). Motor dominant neurons require no visual input and therefore discharge in either the light or dark. Visuomotor neurons respond more strongly in light, but also in dark when neither the hand nor target remain visible. Finally, visual neurons only respond in the light, and some appear to selectively represent the 3-D shapes of graspable objects (Murata et al., 1996).

Area F5 contains interleaved representations of the fingers, hands, and mouth. Cells within F5 appear to be involved in the preparation and execution of visually guided grasping actions (Rizzolatti et al., 1988). This area is subdivided into F5ab, in the posterior bank of the inferior arcuate sulcus, and area F5c, located in the dorsal convexity (Rizzolatti and Luppino, 2001). Both subdivisions receive major inputs from secondary somatosensory cortex (area SII), and IPL area PF (Godschalk et al., 1984b), the latter of which also contains a representation of the face and arm. Area F5ab also receives a major projection from AIP. Like visual neurons in AIP, some F5ab units respond selectively to 3-D shapes even when no hand movements are involved (Sakata et al., 1997). Effective stimuli are typically of a shape that is compatible with a cell's preferred hand configuration (Rizzolatti et al., 1996a). It has been suggested that these visual units code objects' 3-D features and are involved in the selection of appropriate grasping and manipulation movements (Luppino et al., 1999, p. 181). Similar to cells in the anterior superior temporal sulcus (STS) (Jellema et al., 2000), many F5c units appear to represent specific body movements. Specifically, many cells in F5c selectively represent specific hand configurations, e.g., power or precision gripping. However, unlike STS neurons, F5c cells do not code arbitrary postures or movements. Instead, they appear to represent the goal of, rather than the specific movements involved in, manual actions,

e.g., holding, grasping, or tearing an object, and in this sense are context dependent. For instance, if the same hand movement is made in the context of a different action, say grooming instead of feeding, F5c units responses will be weak or absent (Rizzolatti and Luppino, 2001). In short, together with area AIP, F5c neurons appear to represent schemata for particular grasping actions.XX

Until recently, identification of a putative AIP–F5 homologue associated with grasping in humans has proven challenging. Many of the early positron emission tomography (PET) studies observed that grasping was associated with a site in the superior frontal gyrus (BA6) that is a putative homologue of area PMd in the monkey (Grafton et al., 1996; Rizzolatti et al., 1996b). Grafton et al. (1996) suggested that difficulties identifying an AIP–F5 homologue may be related to methodological limitations including use of relatively undemanding tasks and/or reliance on the limited spatiotemporal resolution of PET. More recent work in fMRI appears to support this interpretation. Binkofski and colleagues observed significant bilateral activations within the anterior IPs (putative AIP homologue) when subjects grasped vs. pointed at rectangular visual objects (Fig. 2). Likewise, lesions in this region were also shown to produce deficits in configuring the hand to engage objects (Binkofski et al., 1998). Moreover, haptic exploration of complex vs. simple shapes without vision induced significant activations in putative AIP as well as BA44 (putative F5) (Binkofski et al., 1999). This observation raises the possibility that the circuit is involved in visuomotor and somatomotor transformations during grasping. Put differently, schemata for grasp may be poly-modal.

In an attempt to more closely approximate task demands that activate monkey AIP–F5 neurons, we recently undertook an fMRI study of visually guided grasping using a more varied set of stimuli that have geometrically irregular bounding contours. Using similar objects, Goodale and colleagues demonstrated that subjects adopt stable precision grasps where opposing forces of the thumb and forefinger pass directly through objects' centers of mass (Goodale et al., 1994). Our subjects also showed this pattern when they were required to grasp visually presented versions with their dominant right hands. Compared with a task where subjects pointed at the

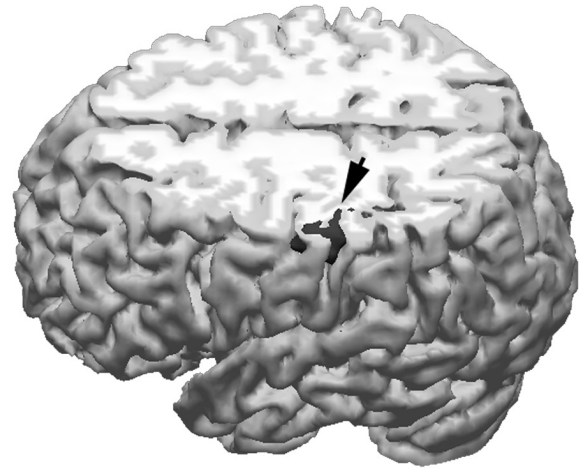


Fig. 2. Probable location of human homologue of area AIP (defined in non-human primates). The black area (indicated by the black arrow) is activated during grasping of objects compared to pointing at objects. The area shown represents the overlap of 90% of subjects ($n = 12$) performing the task with the contralateral right hand. The site is located in the most anterior portion of the intraparietal sulcus, near the junction with the post-central sulcus (Talairach coordinates $-45, -35, 43$).

same objects, grasping activated a putative AIP site in the anterior region of the contralateral IPs as well as the secondary somatosensory region (SII), which also projects directly to F5 in monkey. The center of the AIP site was within 3 mm of what Binkofski et al., observed in their smaller study group. We found remarkable consistency in a very localized area across subjects suggesting that localization of this function is highly consistent across humans. Notably absent in our study are activations in inferior frontal gyrus (GFi, putative homologue of F5). The reason(s) for this is unclear but may have to do with the subtractive comparisons used between pointing and grasping. It is also worth noting that unlike Binkofski et al., we only observed IPs activation in the contralateral hemisphere. Further work on this problem is clearly needed; however, these results suggest that like monkeys, the transformation of objects' intrinsic spatial properties into hand configurations for grasping visual objects in humans involves a highly localized region of the anterior IPs.

To summarize, results of electrophysiology and functional imaging studies converge on the hypothesis that schemata for reaching versus grasping are constructed in two separate parietofrontal circuits in

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the primate brain. Further support for this hypothesis comes from observations of patients with parietal lesions resulting in optic ataxia (OA) vs. ideomotor (IM) apraxia.

Patients with optic ataxia (OA) tend to have troubles *acting on* perceptually available objects. Most investigations suggest that the common locus of damage across OA patients is the SPL, and that the deficit can occur following unilateral lesions in either hemisphere. Patients with left SPL lesions tend to show a ‘visual field effect’: misreaching when they are required to engage objects positioned in the contralesional hemisphere. By contrast, patients with right SPL lesions often display a ‘hand effect’: misreaching when using the contralesional hand to acquire objects located in either hemisphere (Perenin and Vighetto, 1988).

Consistent with observations in monkeys that reaching and grasping are controlled by separate parietofrontal circuits, some OA patients display deficits in visually guided reaching, while still retaining the ability to correctly preshape the hand when grasping (Tzavaras and Masure, 1976). Conversely, grasping can also be affected while reaching remains intact (Jakobson et al., 1991). Recent work in monkey electrophysiology suggests that misreaching resulting from SPL lesions may reflect a failure of parietal neurons to integrate eye and hand position signals (Battaglia-Mayer et al., 2001). Normally, this combined information would be available to premotor areas involved in action planning that receive SPL projections. However, as a result of their SPL lesions, OA patients fail when tasks demand combining eye and hand position information in order to manually engage visual objects. These lesions may therefore impair not just parietal functions, but also the complex interplay between parietal and premotor areas during reaching and grasping actions.

Parietofrontal circuits for acting with objects

Representing the workspace

Reaching and grasping are but the first steps in object, or tool, utilization. It is also essential to relate one’s limbs to the proximal environment. Recent work suggests that visuotactile representations of peripersonal space may be constructed in a circuit

connecting IPL area VIP with PMv area F4 (Fogassi et al., 1992, 1996). Area F4 contains a representation of the face, neck, trunk, and limbs and lies caudal to F5. The majority of units in F4 are bimodal, having tactile receptive fields (RFs) that are in register with 3-D visual RFs of space immediately adjacent to the animal. Importantly, these representations are unaffected by variations in gaze direction. Similar RF properties can be found in area VIP neurons (Colby et al., 1993; Duhamel et al., 1998), which provide direct afferent input to F4 (Luppino et al., 1999). These observations have prompted the hypothesis that the VIP–F4 circuit represents peripersonal space in a frame of reference centered on the body part involved in a given visually guided action (Graziano et al., 1994, 1997; Fogassi et al., 1996).

In point of fact, there are neurons distributed throughout the IPs that appear to have visuotactile properties similar to those observed in area F4. Interestingly, the visual RFs of these units appear to *increase* when monkeys use tools to retrieve other objects (i.e., food pellets). Visual RFs normally in register with tactile RFs of the hand expand to encompass peripersonal space occupied by the tool. Such expansion is not observed when tools are merely manipulated, only when they are actively used to accomplish an intentional action (retrieval of food) (Iriki et al., 1996). Similarly, a recent PET study of monkeys showed increased activation that included VIP and PMv, as well as basal ganglia, pre-SMA, and cerebellum when monkeys used a tool to retrieve food (Obayashi et al., 2001). In a recent pilot study, we used fMRI to compare areas activated when performing a repetitive object transfer task using either the right hand or a handheld set of tongs, as shown in Fig. 3. Using tongs to transfer a set of rings from one peg to another resulted in increased activation within the contralateral inferior frontal gyrus (GFi, putative PMv, i.e., F4). This may reflect an expansion in the representation of the hand to encompass peripersonal space covered by the tool, and additional work is underway to investigate this possibility.

Representing the task

The ultimate challenge of tool use is to retrieve an action representation that matches the specific goal of a

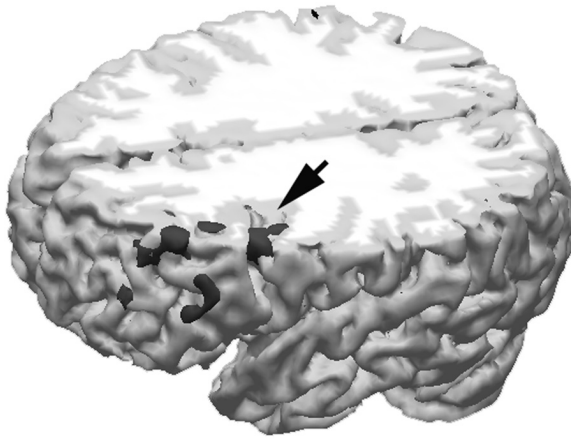


Fig. 3. Acting with tools: remapping the peripersonal workspace. The black area, indicated by the black arrow is within the inferior precentral sulcus. This site was activated during fMRI when a subject transferred objects with a set of tongs that extended the reach of the subject, compared to a control scan of transferring the objects with the fingers. This area may correspond to the ventral premotor area as defined in non-human primates. Neurons in this area in monkeys represent visuotactile properties (Graziano et al., 1997).

task. Over a century of evidence in the neurological literature suggests that retrieval of actions associated with tools involves a system that is functionally and anatomically dissociable from that which controls dexterous prehension, i.e., the acting on system. As elaborated above, patients with OA have difficulties using visual information to control manual actions, regardless of their familiarity with the task. Despite substantial difficulties with on-line prehension to arbitrary objects, however, at least some patients may still accurately acquire familiar objects (Jeanerod, 1994). This astounding observation suggests that the areas involved in reach and grasp can be damaged without disrupting the retrieval and execution of learned skills. In other words, schemata for *acting on* might appear abnormal, while those for *acting with* a familiar object can be relatively intact! This finding has been interpreted as evidence that dorsal and ventral visual streams are interactive; that stored representations of familiar objects' physical properties could be used as cues for prehension by the damaged dorsal stream via their reciprocal interconnections. However, we suggest that this evidence might instead reflect the existence of two dissociable systems of action schemata for within the parietal

lobe: the acting on system that relies exclusively on the physical properties of objects (acting on) and is impaired in OA, and the acting with system that has access to stored utilization information, and may remain intact following SPL damage. The fact that patients with ideomotor apraxia (IM) manifest the reverse dissociation, suggests that intact use of familiar objects in some OA patients is not simply a matter of differences in task difficulty.

Patients with ideomotor (IM) apraxia often appear relatively normal when controlling movements on-line, but are selectively impaired at tasks that require accessing representations of skilled actions, most notably tool use. IM apraxia patients have difficulties that may include one or more of the following: pantomiming tool-use actions, gesturing to command, imitating movements, and in some instances actually using tools or objects (for a comprehensive review see Heilman and Rothi, 1997). At the turn of the previous century, Leipmann showed that right hemisphere damage did not result in apraxia, while a large number of left hemisphere patients were apraxic even when performing movements with the non-hemiplegic, left hand (Leipmann, 1900; Geschwind, 1965; see review in Leiguarda and Marsden, 2000). In contrast to OA patients, IM apraxics commonly exhibit intact reaching and grasping (*acting on*), while failing to correctly retrieve actions associated with familiar tools. For instance, Sirigu et al. reported that left parietal patient LL, committed errors when grasping common objects in order to use them. However, the same objects were grasped correctly when she was simply asked to reach for and grasp them. In other words, LL was capable of performing the visuomotor transformations necessary for accurate prehension. Nevertheless, she could not control her actions based on schemata associated with objects' functions (Sirigu et al., 1995). In short, the contrasting deficits displayed by OA vs. IM apraxic patients suggest the existence of two functionally independent systems for mediating intentional actions (e.g., Buxbaum, 2002). From the perspective of schema theory, these disorders support the existence of two systems of schemata subserving object-oriented actions: one for *acting on* and another for *acting with* objects.

In his original work on IM apraxia, Leipmann hypothesized that schemata, or 'engrams', for skilled

action are stored in the left IPL, specifically the supramarginal gyrus (BA40). A recent analysis of patients with IM apraxia, revealed that damage tended to co-occur within and adjacent to the left IPs including BA 7, angular (BA 39), and supramarginal (BA 40) gyri. In addition, some patients showed damage within the medial frontal gyrus as well (Haaland et al., 2000). Inferring functional localization from lesions is limited by the fact that nature's experiments' do not respect functional boundaries. Therefore, it is difficult to know whether patterns of overlap include tissue that is not directly associated with the behavioral impairment of interest, but instead happens to be damaged along with critical areas as a result of quirks in the cerebral vasculature. In an attempt to overcome these limitations, we recently undertook to evaluate Leipmann's classic hypothesis with fMRI (Johnson et al., 2002).

Common bedside screening for IM involves having the patient attempt to pantomime familiar actions including tool use. For instance, the patient might be asked to demonstrate how she would use a comb, or a hammer. Success on this task demands (1) processing linguistic stimuli in order to recognize the stimulus object, (2) identifying the action associated with the tool, (3) accessing the proper movement representations corresponding to that tool use action, and (4) implementing the correct manual action. We attempted to duplicate this test with the goal of isolating those brain areas specifically involved in accessing representations involved in tools use. Each trial in this randomized, event-related, design consisted of the following three components: (1) an instructional cue (IC); (2) a delay period of either 3 or 5 s; and (3) a movement cue (MC). On 50% of trials, ICs named familiar items that were commonly manipulated in a characteristic way with the dominant hand (e.g., knife, hammer, or pencil). When hearing one of these object ICs, subjects used the delay interval to prepare to pantomime the associated action. If the subsequent MC was a go signal, they executed the pantomime. If the MC was a no-go signal, they merely relaxed until the next IC occurred. An equal number of randomly intermixed trials began with the IC 'move'. During the delay interval on these control trials, subjects simply prepared to move their hand in a random fashion. If the MC was a go signal, they would then execute the random

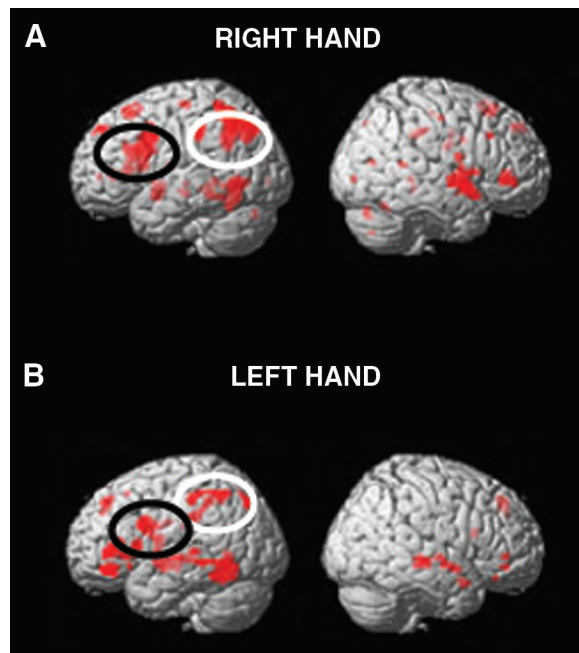


Fig. 4. (A) Areas involved in representing schemata for tool use involving the right hand. When subjects plan tool use actions involving the right hand, substantial activation of the left IPL (white circle) and GFm (black circle) are observed. Homotopic areas are not significantly activated in the right hemisphere. (B) Areas involved in representing schemata for tool use involving the left hand. Planning tool use actions involving the left hand also activate left IPL and GFm, but not homotopic regions in the right hemisphere. Together these results indicate a left hemisphere specialization for representing tool use actions.

movements. If it was a no-go signal they would do nothing. All cues were auditory, and eyes remained closed throughout the task.

In our initial experiment, subjects used their dominant right hands to produce all pantomimes and movements. Of primary interest were those areas activated during the delay interval when subjects were retrieving a tool-associated schemata vs. preparing a random, non-meaningful, hand movement. As predicted by Leipmann over a century ago, Fig. 4A shows that we observed significant activation of the left IPL. However, this included not only BA40 but also extended into the angular gyrus (BA 39) IPs. This pattern is generally consistent with Leipmann's claim that the left IPL plays a key role in storage of schemata for skilled actions. In addition, as reported in the lesion localization literature (Haaland

et al., 2000) we also observed activation of left GFm in the majority of subjects. This pattern suggests that schemata for tool use may be distributed within this parietofrontal network, which is distinct from the more dorsal pathways involved in reaching and grasping discussed above. The involvement of GFm is particularly interesting as this area is closely linked to categorical knowledge about tools (Martin et al., 1996; Grafton et al., 1997; Chao and Martin, 2000). One possibility is that the action representations are stored within the parietal cortex but accessed via computations performed in the premotor regions of the frontal lobe.

A potential limitation of our initial experiment is that subjects always prepared and sometimes produced gestures using their dominant right hands. Consequently, left-lateralized activations in IPL and GFm may reflect a contralaterally organized system for representing tool use, rather than a true left hemisphere specialization. If so, then requiring subjects to prepare gestures for the left hand should induce a shift of activations to the right hemisphere. In a follow-up experiment we replicated the first study except that subjects were now required to prepare and produce gestures with their non-dominant left hands. If the left IPL stores schemata for skilled actions regardless of the effector system, then we should observe a pattern of activity that is very similar to the initial study, i.e., left parietofrontal activations during action retrieval. Fig. 4B shows that our data are highly consistent with this prediction. Both left IPL and GFm were activated during gesture preparation for the left hand. However, there does appear to be some segregation of left- and right-hand related activations within these general regions.

To summarize, our fMRI studies suggest that the left cerebral hemisphere of right-handers is functionally specialized for representing tool use. We are presently investigating whether this is true of left-handers as well. These representations are realized in a network of areas distributed across frontal and parietal cortex. Importantly, this network overlaps minimally with areas of parietal and premotor cortex involved in the online control of reaching, grasping and manipulating objects on the basis of their perceptual attribute. In short, we establish the existence of functionally and anatomically dissociable systems involved in the control of acting with vs. acting on

objects. A key point here is that in the course of actually using tools, we would expect both systems to be involved. As noted at the outset, effective tool use requires both the visuomotor transformations of the acting on system as well as the representations for skilled action computed within the acting with system.

Conclusions

In this chapter we have argued for the applicability of schema theory for understanding the functional substrates of object-oriented actions. Specifically, we proposed that object-oriented actions are guided by two functionally and anatomically distinct representational systems, each specialized for computing different schemata. The *acting on* system involves contralaterally organized, parietofrontal circuits specialized for performing the visuomotor transformations necessary for reaching, grasping, and manipulation of objects on the basis of their perceptual attributes. This system appears to be similarly organized in human and non-human primates. By contrast, the *acting with* system involves the IPL and GFm of the left cerebral hemisphere and represents schemata for skilled tool use that have been acquired gradually over extended periods of time. This latter system may be a specialization of the human brain. Like all models of complex behavior, this proposal is guilty of considerable oversimplification. However, our hope is that it effectively illustrates how the long-lived notion of the action schema might still have relevance today for researchers seeking to integrate knowledge across various disciplines in order to understand better how the brain represents action.

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QUERIES:

?#1: Desmurget, Nat. Neuro., 2000?? (page 130)

?#2: Is this the appropriate location for call-out to Fig. 2 (page 132)

?#3: Update? (page 137)

?#4: Editors? (page 138)