

WHAT PUTS THE HOW IN WHERE? TOOL USE AND THE DIVIDED VISUAL STREAMS HYPOTHESIS

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ABSTRACT

An influential theory suggests that the dorsal (occipito-parietal) visual stream computes representations of objects for purposes of guiding actions (determining ‘how’) independently of ventral (occipito-temporal) stream processes supporting object recognition and semantic processing (determining ‘what’). Yet, the ability of the dorsal stream alone to account for one of the most common forms of human action, tool use, is limited. While experience-dependent modifications to existing dorsal stream representations may explain simple tool use behaviors (e.g., using sticks to extend reach) found among a variety of species, skillful use of manipulable artifacts (e.g., cups, hammers, pencils) requires in addition access to semantic representations of objects’ functions and uses. Functional neuroimaging suggests that this latter information is represented in a left-lateralized network of temporal, frontal and parietal areas. I submit that the well-established dominance of the human left hemisphere in the representation of familiar skills stems from the ability for this acquired knowledge to influence the organization of actions within the dorsal pathway.

Key words: tool use, parietal lobe, left hemisphere, manual prehension, visual streams

SIMPLE AND COMPLEX TOOL USE

In our work we define tools as manipulable objects that are used to transform an actor’s motor output into predictable mechanical actions for purposes of attaining specific goals (i.e., *motor-to-mechanical transformations*). According to this definition, animals ranging from birds (Lefebvre et al., 2002) to elephants (Hart et al., 2001) to a variety of primates are tool users. A lesser number of species are also known to manufacture tools for specific functions, including crows (Hunt, 1996), orangutans (van Schaik et al., 2003), monkeys (Westergaard and Suomi, 1994) and chimpanzees (Boesch and Boesch, 1990). These behaviors almost always involve what is known as extractive foraging – using objects to obtain food items that are otherwise inaccessible (van Schaik et al., 1999). These *simple tool use behaviors involve using objects to implement motor-to-mechanical transformations that amplify movements of the upper limbs* (e.g., using a rock to increase pounding force, or a stick to extend reach). Simple tool use generally involves modest modifications of objects that occur with frequency in the animals’ environments, and are limited to specific subgroups within a species; i.e., are not defining characteristics of the species. For instance, only some tribes of chimpanzees are known to use stones as hammers and anvils to crack nuts (McGrew et al., 1997). It is also noteworthy that the relative sizes of stones chosen as hammers or anvils vary considerably, and their roles can be interchanged (Sakura and Matsuzawa, 1991).

Likewise, the procedures involved in manipulating stones differ among individuals.

By contrast, *complex tool use involves using objects to implement transformations that convert movements of the hands into qualitatively different mechanical actions* (e.g., using a knife to cut, a pencil to write, or brush to cleanse the teeth). There are reasons to believe that the brain represents simple *versus* complex tool use behaviors differently. First, although humans also engage in acts of simple tool use (e.g., using tweezers to extend the pincer grip), we are the only animals known to possess a vast repertoire of complex tool use skills. Only hominids manufacture compound tools (artifacts) by joining together multiple parts and/or materials, and there is no evidence indicating that non-hominids make one tool in order to create another (e.g., shaping a rock cutter to manufacture a wooden spear). This has been taking place for a relatively long time; the available fossil record indicates that ancestral hominids were using rocks to manufacture stone cutting implements about 2.5 million years ago (Ambrose, 2001). Second, complex tools have been manufactured to improve their functionality in ways that suggest the existence of well-defined plans, or mental schemata. Third, unlike many simple tools, complex tools typically have very narrowly-defined functions that are therefore not interchangeable (e.g., toothbrushes, writing instruments, and eating utensils). Fourth, although the precise tools may differ depending on needs, complex tool use is a universal and defining trait of all human cultures. Finally, highly refined procedures for skillful use

have co-evolved with complex tools, and are actively transmitted to successive generations.

A fundamental and unresolved question concerns the brain mechanisms underlying simple and complex tool use, and how they account for similarities and differences in the behaviors of human and non-human tool users. One place to begin is with a closer look at the organization of systems involved in object perception and manual actions in primates.

THE WHAT AND HOW OF TOOL USE

It is widely accepted that extrastriate visual areas in non-human primates are grossly organized into two anatomically dissociable processing streams: one extending ventrally from occipital into inferior temporal cortex, the other extending dorsally from occipital into posterior parietal cortex (Felleman and Van Essen, 1991). Ample opportunities for direct and indirect interactions between these streams exist. Rostral superior temporal sulcus (STS) receives input from posterior areas in both pathways (Ungerleider, 1995), and direct reciprocal interconnections between areas within these streams provide a means for cross-talk (Morel and Bullier, 1990; Young, 1992). Further, many areas within the dorsal and ventral streams are also reciprocally interconnected with areas of prefrontal cortex known to be involved in various executive functions including working memory and action planning (Wilson et al., 1993). Areas of the dorsal stream project to Brodmann area (BA) 46 in the principal sulcus, an area that appears to represent the locations of objects in space. Conversely, ventral stream areas are connected with BAs 12 and 45 located in the inferior frontal convexity that appear to represent objects' identities (Goldman-Rakic, 1996a, 1996b). Feedback via these reciprocal connections may enable prefrontal structures to influence processing within the dorsal and ventral streams.

Of relevance to the issue of tool use is evidence indicating that these pathways differ in terms of the information they represent. The traditional view is that objects' intrinsic attributes (e.g., shape, orientation, color, and texture) are processed within the ventral ('what') stream separately from their extrinsic spatial properties (locations and movements) that are analyzed in the dorsal ('where') stream (Mishkin et al., 1983; Ungerleider and Mishkin, 1982; Ungerleider and Haxby, 1994). The highly counterintuitive nature of this proposal is part of its attraction. From a phenomenological stance, objects' identities and the locations they occupy are inseparable: we never perceive objects that do not appear to be located somewhere in our environment. Likewise, as elaborated below, in order to successfully coordinate skilled actions we must construct accurate representations of *both* what objects are and where they are located.

More recently, Goodale and colleagues (Goodale et al., 1991, 1994; Culham et al., 2003; James et al., 2003) have argued that both the ventral and dorsal streams are involved in processing objects' intrinsic and extrinsic properties, but for *different purposes*. The ventral stream is said to compute intrinsic properties necessary for object recognition and semantic processing (i.e., determining 'what'), while the dorsal stream is thought to recover *both* intrinsic and extrinsic attributes for purposes of guiding actions (i.e., determining 'how'). Observations of patient D.F., who became profoundly agnostic following bilateral damage to the ventral stream, clearly illustrate this distinction (Goodale et al., 1991). Despite an inability to judge objects' shapes, sizes, and orientations consciously, D.F. is capable of using aspects of this information to preshape and orient her hand correctly during visually-guided prehension. With respect to simple tool use, D.F. is also able to orient and post a handheld card through a narrow slot despite an inability to judge the target's orientation accurately. D.F.'s success with these manual actions is considered evidence that her intact dorsal stream is capable of processing intrinsic and extrinsic object properties for the purpose of controlling visuomotor behaviors (Goodale et al., 1991; Milner and Goodale, 1995).

While alternatives to the Milner and Goodale (1995) model do exist (Creem and Proffitt, 2001a; Glover, 2004; Jeannerod, 1994; Jeannerod and Jacob, 2005), it is clear that dissociations between ventral and dorsal stream functions have profoundly altered our understanding of the relationship between perception and action. A truly comprehensive theory of human action must, however, address not only sensory-guided actions (e.g., reaching, grasping and object manipulation), but also acquired skills, including the dexterous use of familiar tools. Yet, a treatment of these behaviors has been conspicuously absent from this discussion. One possibility is that tool use abilities arise from extensions of dorsal stream (i.e., parietal) representations involved in visually-guided actions. Consistent with this hypothesis, electrophysiological evidence demonstrates expansions of receptive fields in visuo-tactile parietal neurons that represent the upper limb when highly trained macaques use simple tools (rakes) to extend their reaches (Iriki et al., 1996; Ishibashi et al., 2002; Obayashi et al., 2001). Psychophysical evidence from healthy (Maravita et al., 2001, 2002) and brain-injured (Berti and Frassinetti, 2000; Berti et al., 2001; Farne and Ladavas, 2000) humans also suggests that reaching with simple tools is accompanied by an expansion of one's representation of peripersonal space (Maravita and Iriki, 2004). In other words, this work indicates that acquisition of simple tool use skills induces experience-dependent modifications of existing limb representations within the dorsal stream.

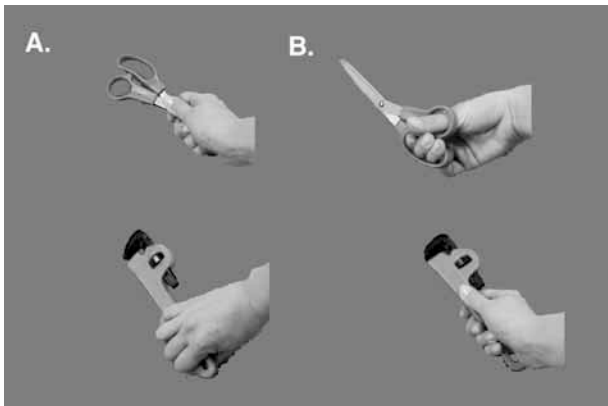


Fig. 1 – The distinction between actions based on objects' perceived versus acquired affordances. A) A scissors and wrench held in stable grips that can be achieved on the basis of sensory-motor transformations alone. B) The same objects grasped in ways that are consistent with their known functions. These postures reflect access to stored semantic attributes.

While this dorsal stream hypothesis may provide a good explanation for the neural bases of simple tool use behaviors, it is insufficient to explain complex human tool use. To wit, although agnosic D.F. can grasp and manipulate objects on the basis of their physical properties, she does so in a manner that is not necessarily compatible with their acquired usage (Carey et al., 1996). Likewise, apraxics who have difficulties representing acquired skills may be surprisingly accurate when grasping and manipulating familiar objects on the basis of their 3-D structural properties, even when failing to use such objects appropriately for their learned functions (Buxbaum et al., 2003; Sirigu et al., 1995). Such patients may also retain the ability to infer novel objects' uses from their physical attributes (Goldenberg and Hagmann, 1998). While some have ascribed apraxia to an impairment of the dorsal stream (Leiguarda and Marsden, 2000), these findings suggest otherwise: sensory-motor control may remain relatively intact, while the ability to undertake actions in a manner that is sensitive to semantic knowledge is compromised. The differences between these two routes for action are illustrated in *Figure 1*. A variety of different postures can be used to achieve a stable grip that will enable an actor to grasp familiar tools stably for purposes such as moving them from one location to another, or handing them to another individual (Figure 1A). These examples reflect successful transformations of representations of objects' intrinsic and extrinsic spatial properties and the limb into motor programs for prehension. While modifications to such sensory-motor transformations may account for simple tool use actions, these solutions are clearly not suitable for using familiar artifacts to perform their ordinary functions. Grips appropriate for tool use frequently differ in non-trivial ways from those chosen solely on the basis of sensory information (Figure 1B). In addition to mechanisms for on-line sensory-to-motor transformations, the actions of the complex tool user are influenced by semantic

knowledge of objects' functional properties and uses. Both sensory-motor and semantic representations are necessary for successful complex tool use, yet neither alone is sufficient. The key to understanding complex tool use is to determine how semantic knowledge, represented at least in part within the ventral stream, is integrated with sensory-motor representations within the dorsal stream (Buxbaum, 2001; Creem and Proffitt, 2001b; Johnson-Frey, 2003a, 2003b; Johnson-Frey and Grafton, 2003; for a computational perspective on these interactions see Fagg and Arbib, 1998).

FUNCTIONAL NEUROIMAGING STUDIES OF TOOL KNOWLEDGE AND USE

A recent review of available neuroimaging data examined brain areas activated during semantic tasks (e.g., object naming or classification) involving tools *versus* those regions associated with planning to execute familiar tool use actions (Johnson-Frey, 2004; see also Lewis, 2006). Of direct relevance to the current argument are two observations. First, activations associated with either semantic or action planning tasks are highly lateralized to the human left cerebral hemisphere. This is distinguished from the apparent contralateral organization of dorsal stream mechanisms involved in visually-guided prehension (Binkofski et al., 1998; Culham et al., 2003; Johnson-Frey et al., 2005c). Although not discussed in detail here, these findings are also highly consistent with the long-standing association between left hemisphere damage and apraxia (Basso et al., 1980; Goldenberg, 2003; Haaland et al., 2000; Heilman and Rothi, 1997). Apraxics have difficulties imitating and/or gesturing skilled actions, including the use of familiar tools that cannot be attributed to elemental sensory or motor deficits.

Second, despite having very different output demands, cortical areas activated during either semantic or tool use planning tasks overlap considerably. Even though movements are neither planned nor executed, semantic tasks involving familiar tools activate a distributed network in the left hemisphere including areas within the ventral (posterior temporal cortex) *and* dorsal (inferior parietal lobule – IPL) streams¹, as well as frontal

¹While the IPL and SPL in macaques are both considered parts of the dorsal processing stream, classification of the IPL in humans is a matter of speculation at present. Goodale and Milner (1995) suggest that, on the basis of its involvement in certain cognitive tasks (e.g., mental rotation), IPL might belong to the ventral stream. However, this argument is circular. I have thus taken the conservative stance of treating the entire human parietal lobe as part of the dorsal stream. The ultimate classification of human IPL will be based on anatomical connectivity data that is not yet available. It is known that the anterior region of the IPL adjacent (PF) and within the intraparietal sulcus (AIP) in question is involved in the visual control of grasp in macaques (Sakata et al., 1995; Gallese et al., 1994). fMRI data indicates a putative homologue in humans (Binkofski et al., 1998; Culham et al., 2003; Johnson-Frey et al., 2005c). However, given the limited spatial resolution of this technique it is difficult to differentiate regions within the IPS that belong to the IPL *versus* SPL.

cortex (inferior and/or middle frontal gyri) (Chao et al., 1999; Damasio et al., 2001; Kellenbach et al., 2003; Martin et al., 1995, 1996). Likewise, planning to execute tool use skills activates areas within the dorsal stream (IPL and/or superior parietal – SPL – lobules) (Choi et al., 2001; Moll et al., 2000; Ohgami et al., 2004; Rumiati et al., 2004), premotor (Choi et al., 2001; Moll et al., 2000; Rumiati et al., 2004) and/or prefrontal (Choi et al., 2001; Moll et al., 2000) cortices. In addition, activation of the ventral stream (posterior temporal cortex) has also been noted when familiar tool use actions were being planned (Choi et al., 2001)². As discussed in detail below, recent work in our lab also detects ventral stream activation in the left hemisphere when planning tool use actions (Johnson-Frey et al., 2005b).

The presence of dorsal stream activity during action semantic tasks and ventral stream activity when planning familiar actions is consistent with the hypothesis that both streams are involved in representing information necessary for complex tool use. It has previously been suggested that both streams play a role in representing semantic information associated with these objects, including actions involved in their manipulation (Chao and Martin, 2000; Martin and Chao, 2001). As with other types of semantic information (Allport, 1985), representations of manipulable objects may involve those brain regions that are active at the time of encoding. These would include temporal areas activated during the perception of visual properties associated with tools and their movements (Beauchamp et al., 2002; Chao et al., 1999), as well as any parietal and premotor areas active during their manipulation (Chao and Martin, 2000). The left-lateralization of these parietal-premotor responses might reflect the fact that most individuals have a rich history of using these objects with their contralateral right hands. However, there is evidence suggesting that tool use skills are represented predominantly in the left hemispheres of even left-handed individuals (Johnson-Frey et al., 2005a; Lausberg et al., 1999; Raymer et al., 1999; however see Lewis et al., 2006). Alternatively, this cerebral asymmetry may reflect the inter-relationship between representations of these acquired skills and left hemisphere semantic processes more generally.

SEPARATING AREAS INVOLVED IN PLANNING VERSUS EXECUTING TOOL USE SKILLS

In an attempt to clarify these issues, we recently undertook two randomized, event-related functional

magnetic resonance imaging (fMRI) studies with the goal of identifying areas active during planning and/or execution of familiar tool use actions (Johnson-Frey et al., 2005b). Healthy, right-handed adults participated in two separate studies using either their right (Experiment 1) or left (Experiment 2) hands. To eliminate effects associated with bottom-up visual processing, stimuli were object names presented aurally and subjects' eyes remained closed throughout the experiments. On experimental trials, subjects received cue words identifying familiar tools/utensils, and were instructed to plan unimanual actions associated with using the objects. Following a variable length delay interval subjects received a GO signal instructing them to execute the planned action on half of the trials. On the remaining "catch" trials subjects were required to retrieve and plan tool use actions, but then received a NOGO cue instructing them not to execute. These trials provided us with a pure measure of premovement activation. Control trials also consisted of GO or NOGO versions. However, here subjects prepared meaningless hand movements of their choosing in response to the cue word "move". To minimize motion-related effects, all movements were constrained in amplitude and involved only the hand, wrist and forearm.

In accordance with the view developed here, we had two predictions: first, regardless of the limb involved, activations associated with planning tool use gestures would be found in both dorsal and ventral stream regions within the left cerebral hemisphere. On the basis of earlier work on action semantics, we expected left posterior parietal cortex, posterior temporal, and ventral premotor cortex to be involved. Of particular interest was determining whether any additional regions not observed previously during semantic processing would be noted in association with this action planning task. Such differences might reflect (an) area(s) involved in the integration of semantic and sensory-motor information. Second, execution of these gestures would involve regions within the dorsal stream bilaterally as well as interconnected regions of premotor cortex. These parieto-frontal circuits represent the sensory-to-motor transformations necessary for the online control of actions.

Figure 2 summarizes those brain regions that were significantly activated across both experiments; i.e., regardless of the limb involved. Relative to the control condition, planning tool use actions in the absence of execution (NOGO conditions) activated four regions all within the left cerebral hemisphere (gray). These included two distinct sites in the IPL, one located in the anterior supramarginal gyrus (SMG) and another in posterior SMG and angular gyrus (ANG). The anterior site is consistent with the locus of activations observed during previous semantic tasks involving tools (Chao and Martin, 2000; Damasio et al., 2001; Kellenbach et al., 2003). By contrast, the more posterior region is consistent

²The region of left posterior temporal cortex activated in a variety of tasks involving tools is near to but distinct from motion processing centers (putative homologues of MT/MST) (Beauchamp et al., 2002). This is an important point because MT-MST in the macaque are considered part of the dorsal visual processing streams.

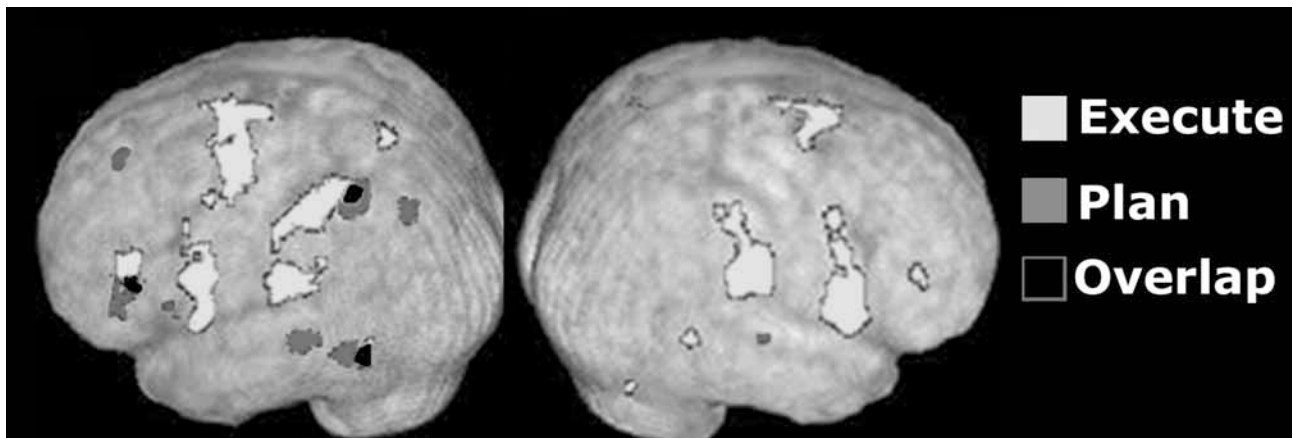


Fig. 2 – Brain areas activated when planning and/or executing complex tool use actions with the right and left hands. White areas were significantly activated when pantomiming familiar tool use actions the right and left hands versus executing random hand movements. Gray areas were activated when planning tool use actions for both the right and left hands versus preparing random hand movements. Black areas were activated when planning and executing tool use actions with the left and right hands. While bilateral regions of frontal, parietal and temporal cortex are all involved in execution, planning complex tool use actions is associated with lateralized activity in the left cerebral hemisphere. There is both segregation and some degree of overlap amongst regions in left inferior frontal, inferior parietal and posterior temporal cortex that contribute to planning and execution. Left dorsolateral prefrontal cortex and right STS activity is only observed during planning and may reflect working memory demands. Modified from (Johnson-Frey et al., 2005b).

with results from two earlier investigations of preparing and executing tool use actions (Choi et al., 2001; Moll et al., 2000). More will be said about this below. Consistent with the lesion data from apraxia (Haaland et al., 2000), the ventral portion of the left middle frontal gyrus was also activated along with inferior frontal and ventral premotor cortices, both of which are implicated in the representation of action-related semantic information (Chao and Martin, 2000; Damasio et al., 2001; Grabowski et al., 1998; Kellenbach et al., 2003; Martin et al., 1996). Unexpectedly, we also observed a focal activation within left dorsolateral prefrontal cortex (DLFPC). Previous work implicates this region in a variety of tasks involving executive control and semantic working memory (Gabrieli et al., 1998; Poldrack et al., 1999; Wagner et al., 2001). It is possible that this area contributes to the coordination of semantic and action representations during the delay interval. As expected, planning familiar tool use skills was also associated with activity in the ventral stream; specifically within the posterior STS and in adjacent regions of the middle and superior temporal gyri, all known to be active during semantic tasks involving action (Chao et al., 1999; Damasio et al., 2001; Martin et al., 1995, 1996). It is worth noting that this activity occurred even in the absence of visual stimulation or bodily motion.

Executing tool use actions with the left or right hands activated a bilaterally organized network (white) that included parietal and premotor areas known to be involved in sensori-guided upper limb movements (Binkofski et al., 1999; Culham et al., 2003; Grafton et al., 1992, 1996; Johnson-Frey et al., 2005c).

Finally, left temporal, posterior IPL and inferior frontal regions active when planning tool use

gestures remained active during movement production (black). This is consistent with these areas playing a role in planning processes that overlap in time with movement execution (Desmurget et al., 1999; Tunik et al., 2005).

A potential criticism of this work concerns the absence of controls for lexical and semantic processing. Perhaps the left lateralization during planning can be ascribed solely to semantic-linguistic functions and has nothing to do with preparing familiar actions? To the extent that *how* objects are grasped and manipulated is actually part of their semantic representations (Chao and Martin, 2000), then distinguishing planning and semantic processing may not be possible. Yet, while most of these sites have been shown to be active during perceptual and/or semantic tasks involving tools, even when no actions were explicitly planned (Chao and Martin, 2000; Martin and Chao, 2001), the more posterior left IPL activation (SMG-ANG) has only been reported during action planning (Grezes and Decety, 2001; Johnson-Frey, 2004). Importantly, this area coincides with the location of maximal lesion overlap in parietal-injured apraxia patients (Haaland et al., 2000), and is distinct from sites involved in motor attention (Rushworth et al., 1997, 2001). This more posterior region of the left IPL may be specifically involved in constructing representations of acquired manual skills on the basis of semantic and sensory-motor information. In the macaque, the IPL receives visual input from posterior temporal cortex (MT/MST) (Rizzolatti and Matelli, 2003). It is conceivable that similar temporal-parietal pathways in humans may facilitate the interaction of semantic and action representations within the IPL.

Recently, Rumiati et al. (2004) reported results of a PET study of tool use pantomimes that did

control for processes involved in movement execution, semantic and lexical processing. Similar to other studies of tool use actions, they observed activations within regions of left IPL and inferior frontal cortex. Absent, however, were activations within the ventral stream, specifically posterior left temporal cortex. On the one hand, this could be interpreted as an indication that the ventral stream areas are not involved in planning familiar tool use actions, but rather participate in semantic processes exclusively. On the other hand, if these regions were activated similarly during both semantic and action planning tasks, then they would be eliminated through subtractive comparisons. The fact that left IPL and frontal areas survive these contrasts suggests that these regions play a greater role in action planning than semantics.

CONCLUSIONS

Any comprehensive theory of human action must account for behaviors, such as complex tool use, that are influenced by retrieval of semantic information (Creem and Proffitt, 2001b; Gentilucci, 2003; Humphreys and Riddoch, 2000; Tucker and Ellis, 1998). Simple tool use behaviors may arise through experience-dependent modifications of the dorsal (where) stream that guides behavior on the basis of objects' 3-D structural properties. Complex tool use behaviors depend in addition on access to representations of objects' semantic properties. This information is implemented within a distributed left hemisphere network including areas within the ventral (what) stream as well as parietal and frontal regions, and specifies *how* these artifacts are used. It is suggested that the posterior left IPL may be a critical juncture for the integration of semantic and sensory-motor information. In short, when it comes to complex tool use, it might be said that "what" puts the "how" in "where".

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