Review TRENDS in Cognitive Sciences Vol.8 No.2 February 2004

The neural bases of complex tool use in humans

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The behaviors involved in complex human tool use cut across boundaries traditionally drawn between social, cognitive, perceptual and motor processes. Longstanding neuropsychological evidence suggests a distinction between brain systems responsible for representing: (1) semantic knowledge about familiar tools and their uses, and (2) the acquired skills necessary for performing these actions. Contemporary findings in functional neuroimaging support and refine this distinction by revealing the distributed neural systems that support these processes and the conditions under which they interact. Together, these findings indicate that behaviors associated with complex tool use arise from functionally specialized networks involving temporal, parietal and frontal areas within the left cerebral hemisphere.

Although many animals use simple tools to extend their physical capabilities, humans are unique in having established a culture in which the manufacture and use of complex tools is a universal feature. In contrast to the simple tools used by other species (e.g. sticks for reaching, rocks for pounding), we create complex artifacts (axes, spoons, pencils) that reflect a deep understanding of the physics of our bodies, surrounding objects, and the unique demands of the external environments in which we live [1]. To our knowledge, we are the only species for whom these artifacts and the skills associated with their usage are refined over successive generations and actively taught to our offspring, that is, transmitted culturally [2].

A fundamental question in human evolution concerns the relationship between phylogenetic changes in the brain and the development of hominid tool manufacture and use [3]. Yet this question has received surprisingly little attention in mainstream cognitive and neuroscience research. Until very recently, our understanding of the functional architecture of complex tool use came exclusively from investigations of behavioral impairments resulting from brain damage. With increasing access to non-invasive functional neuroimaging and a growing concern for studying complex real-world actions, the literature on tool use is undergoing rapid expansion. Results of this work provide an opportunity to evaluate hypotheses generated from patient-based studies in healthy populations and to seek convergence across methods that have their own, often complementary, strengths and weaknesses.

Early and enduring insights from case studies of brain injury

Until very recently, our understanding of the brain mechanisms involved in representing complex tools and their usage came exclusively from studies of brain-injured patients suffering from apraxia – a disorder of learned, voluntary actions, or *skills*. Over a century ago, several European neurologists recognized that brain injury could selectively disrupt various processes necessary for skillful behaviors, including tool use [4,5]. Their observations began a tradition of apraxia research in behavioral neurology and neuropsychology that has yielded several important insights into how the brain represents knowledge about familiar tools and their uses.

Distinguishing between conceptual and production systems

From as early as Morlass in 1928, it has been noted that brain damage could selectively impair conceptual knowledge about tools versus the skills necessary for their dexterous usage (cited in [6]). A schematic summarizing what was known about locations of brain lesions associated with conceptual versus production difficulties during the early 20th century is shown in Figure 1.

When asked to pantomime, or in some cases explicitly demonstrate, how a familiar tool is used, patients with conceptual level difficulties often make ‘errors of content’ in which actions are performed skillfully but out of context. For instance, Ochipa and colleagues report a patient who attempted to brush his teeth with a comb and eat with a toothbrush. This is not due to a failure of object recognition (agnosia) because the individual could identify the objects by name [7]. Content errors indicate that representations necessary for performing tool-use skills are separable from semantic knowledge concerning the relationships between tools and their associated functions [8]. The terms ‘Ideational’ and ‘Conceptual’ Apraxia have been used to refer to this disorder with the latter pertaining specifically to this semantic component [9]. Although lesion data are not entirely unequivocal, these semantic deficits are associated frequently with damage to the left hemisphere at the intersection of the temporal-parietal-occipital cortices [10].

The reverse dissociation also occurs: Ideomotor Apraxics retain knowledge of tools’ functions and associated actions,

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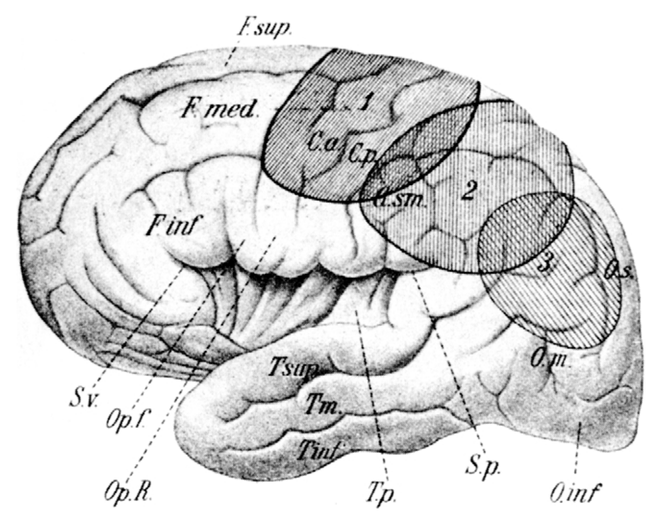

Figure 1. Regions known to affect tool use when damaged. This schematic drawing from the early 20th century illustrates locations of brain lesions in left parietal cortex associated with three forms of apraxia as understood by Liepmann. Damage to Region 1 was associated with Limb-Kinetic Apraxia arising from a disturbance of sensori-motor transformations involved in limb movements. Damage in Region 2 was associated with Ideomotor Apraxia, or difficulties producing acquired motor skills from memory, including tool use. Damage to Region 3 was associated with Ideational Apraxia, or difficulties retrieving conceptual knowledge about tools and the action sequences associated with their uses. There is partial overlap among adjacent regions in recognition that the various forms of apraxia are often not manifest in pure form. Although this figure would appear to suggest a strong localizationist perspective, Liepmann did not believe that representations underlying tool use, or praxis in general, are exclusive to specific brain sites. Rather he believed that they were a product of the whole brain with posterior regions possibly supporting visual representations of planned actions [5]. Reproduced from [20] by permission of Lawrence Erlbaum Associates, Inc.

but nonetheless appear to have lost access to the representations needed to undertake the associated motor skills. Classically, Ideomotor Apraxics have difficulties when asked to pantomime or act out how familiar tools are used on the basis of either visual or verbal cues. The fact that Ideomotor Apraxics often perform worse at pantomime than when using actual objects [11], is often interpreted as a failure to perform volitional actions from memory [4]. It is noteworthy, however, that apraxic patients with left-hemisphere lesions are known to also make errors when demonstrating how tools are used with the actual objects in hand [12]. Moreover, Ideomotor Apraxics are capable of accurately grasping and manipulating tools on the basis of their perceptual properties [13], even when failing to use the very same objects appropriately for their learned functions [14]. This is an important observation because it suggests that acquired skills are also represented independently of the sensori-motor transformations necessary for movement execution [15,16]. Further support for this distinction comes from the fact that young children acquire tool-use skills long after having mastered sensori-motor control of the hands and arms (see Box 1).

Beginning with an early group study by Liepmann and Maas [17], research has shown that virtually without exception Ideomotor Apraxia follows damage to the left posterior parietal and/or premotor cortex, or isolation of the left hemisphere from the right following damage to the corpus callosum [18]. Although this hypothesis is based on right-handers, the left cerebral hemisphere might be specialized for representing tool-use skills even in left-handed individuals [19].

Box 1. The development of tool-use skills in young children

Work in developmental psychology has yielded insights into the development of tool-use skills in young children [60,61] and their understanding of objects' functions [62] that could provide important clues to the nature of underlying neurocognitive mechanisms. An elegant study by McCarty and colleagues illustrates the important role that the development of planning abilities play in the acquisition of a complex tool-use skill [63]. In one study, the authors presented young children (9-, 14-, and 19-month-olds) with spoons loaded with food whose handles alternately pointed in the direction of 3 or 9 o'clock, and observed how they coped with the problem of getting food into their mouths. The youngest children tended to reach with their dominant hand irrespective of the spoon's orientation. By contrast, older children tended to use whichever hand allowed them to grasp the spoon in a comfortable radial grip; that is, with the thumb-side of the hand toward the spoon's bowl. This solution reflects an ability to anticipate the forthcoming demands associated with the goal of the action (i.e. getting the food into their mouths) and adjusting their tool-using movements accordingly. Like adults [64,65], 18-month-old infants appear able to formulate motor plans that extend beyond the immediate spatial constraints of the task, and capture the demands of forthcoming actions. Apparently, this anticipatory planning ability develops somewhere between 9 and 18 months of age. It has been argued that the ability to engage in this sort of causal reasoning is unique to humans, and might be an important component of tool use [66].

In summary, two of the most influential and enduring hypotheses to emerge from the study of apraxia over the last century are that: (i) representations of conceptual knowledge about tools and associated actions are distinct from representations of the acquired skills necessary for dexterous tool use [17,20,21], and (ii) both types of knowledge are represented in dissociable neural systems within the left cerebral hemisphere. Here I evaluate these hypotheses in light of current findings from functional neuroimaging research on the representations of tools and their uses in healthy adults.

Representing knowledge of tools and associated actions

The difficulties experienced by Conceptual Apraxics can be interpreted as stemming from a form of semantic memory deficit [10]. Rothi and colleagues have argued that knowledge about actions, including tool use, might be represented in a specialized 'action semantic system' [22]. In addition, it has been proposed that the semantic system for action be fractionated further into separate subsystems for knowledge about tools, their functions, or how the appropriate actions associated with their uses are sequenced [8].

Although difficulties with semantic access may contribute heavily to these difficulties, it is important to acknowledge that non-semantic processes could also play a role in understanding tool-action relations. Goldenberg and Hagmann demonstrate that apraxics have problems inferring novel tools' functions directly from their perceived structures [6]. Conversely, relatively preserved object use in patients with semantic dementia due to atrophy of the temporal lobes appears to reflect use of this alternative mechanical problem-solving route [23]. It is conceivable that functional neuroimaging could be helpful in exploring the relationship between mechanisms involved in these semantic and non-semantic processes. With respect to the former, insights into the representation of knowledge about tools and their usage can be found in the related literature on semantic memory.

Left posterior temporal cortex and tool identification

Whereas Conceptual Apraxics can accurately name and identify tools, Tranel and colleagues report patients who are particularly impaired at tool naming. Like many Conceptual Apraxics, these patients have lesions that overlap maximally near the intersection of the parietal, occipital and temporal cortices in the left cerebral hemisphere [24]. One interpretation of these data is that this region of the left hemisphere computes distinct representations for naming versus other types of semantic knowledge associated with tools.

Neuroimaging studies in healthy adults specifically implicate posterior left temporal cortex in tool identification. Martin and colleagues [25] found that naming tools selectively activates posterior left middle temporal gyrus (MTG), an area that is also engaged when subjects generate action words [26], or answer questions about tools [27]. Likewise, Damasio and colleagues report activation in this region when subjects identify actions or spatial relations performed with versus without a tool [28].

The relationship between category-specific naming deficits, localized patterns of brain activity, and the functional architecture of conceptual representations is unresolved [29]. Are these activations reflecting the category ‘tool’ *per se*, or some more elemental property common to all members of this category? One account of left MTG activity is that this region is coding perceptual properties associated with tools [28]. But, what specifically is different about tools as compared to other artifacts? On the basis of its proximity to motion processing centers (putative V5/MT) and its selectivity for ‘manipulable’ versus ‘non-manipulable’ artifacts, it has been suggested that activations in left MTG might be involved in representing non-biological motions associated with tool use [27]. The idea that naming a tool could drive these areas seems reasonable given that putative V5/MT can be activated by static images that imply action [30]. Recently, Beauchamp and colleagues demonstrated that posterior MTG is indeed selectively activated when subjects observe the non-biological motion of tools versus the biological motion of human forms [31]. A similar logic has been applied to category-specific activations associated with processing visually presented tools in bilateral, medial fusiform gyrus. It has been suggested that these areas might be involved in the representation of tools’ shapes [27].

The distinction between Conceptual and Ideomotor Apraxia, discussed above, suggests that semantic information about tools and the representations necessary for the production of tool-use skills are constructed in functionally dissociable systems. Nevertheless, behavioral studies of healthy adults [32] and individuals with semantic dementia [33] demonstrate that conceptual representations influence the production of tool-use skills. An important revelation from functional neuroimaging studies, not predicted from studies of brain-injured patients, is that such interactions may come about through *automatic* activation of action representations in premotor and/or parietal areas when semantic information concerning familiar tools is accessed.

Left frontal and parietal cortices and action knowledge

In addition to temporal cortex, functional neuroimaging studies consistently demonstrate that identification of tools and actions activates frontal and parietal areas not typically associated with recognition or semantic access. Activation of left inferior frontal cortex – a region associated with visuomotor transformations for grasping and manipulating objects in both macaques [34] and humans [35] – is observed during tool naming [25,36] and viewing [36], whereas a larger region including, left middle frontal gyrus (GFm) is activated when identifying the actions with which tools are associated [37]. Similarly, Perani and colleagues also observed activation in left dorsal premotor cortex – an area involved in visuomotor transformations for reaching in macaques [38] and humans [39] – during a same/different tool recognition task [40]. Grafton, *et al.* also found left dorsal premotor activity when tools are viewed passively, whereas naming the uses of observed tools additionally recruited left ventral premotor cortex and the supplementary motor area [41]. These passive viewing effects are consistent with behavioral observations showing that tools can preferentially capture visual selective attention [42]. Recent findings suggest that selective responses to tools in dorsal premotor cortex only occur when this capture takes place [43].

The consistent activation of left ventral and/or dorsal premotor cortex during tool naming and/or observation is consistent with automatic engagement of mechanisms involved in the planning of grasping and reaching movements, respectively. Yet, as detailed below, there is considerable evidence to indicate that specific tool-use skills are represented in left posterior parietal cortex (PPC). Although less common, activations in this posterior region are also noted when subjects name tools [25,36] and the actions with which they are associated [28]. One possible reason why these sites are not reported more often in tasks involving tool perception is that they might only be activated when subjects are *explicitly* required to retrieve semantic information concerning tool-use actions [44]. Kellenbach *et al.* observed that visually presented tools engage left ventral premotor cortex and posterior left MTG regardless of whether the retrieval task demands judgments about their functions or associated actions. In other words, responses in these areas are automatically evoked by the mere observation of familiar tools. Conversely, activations in left PPC are only observed when subjects explicitly retrieve actions associated with tools (Figure 2).

Neuroimaging data suggesting automatic activation of frontal and/or parietal areas involved in representing actions during perceptual tasks has implications for interpreting existing findings in the neuropsychology literature as well. For instance, Sirigu *et al.* report an

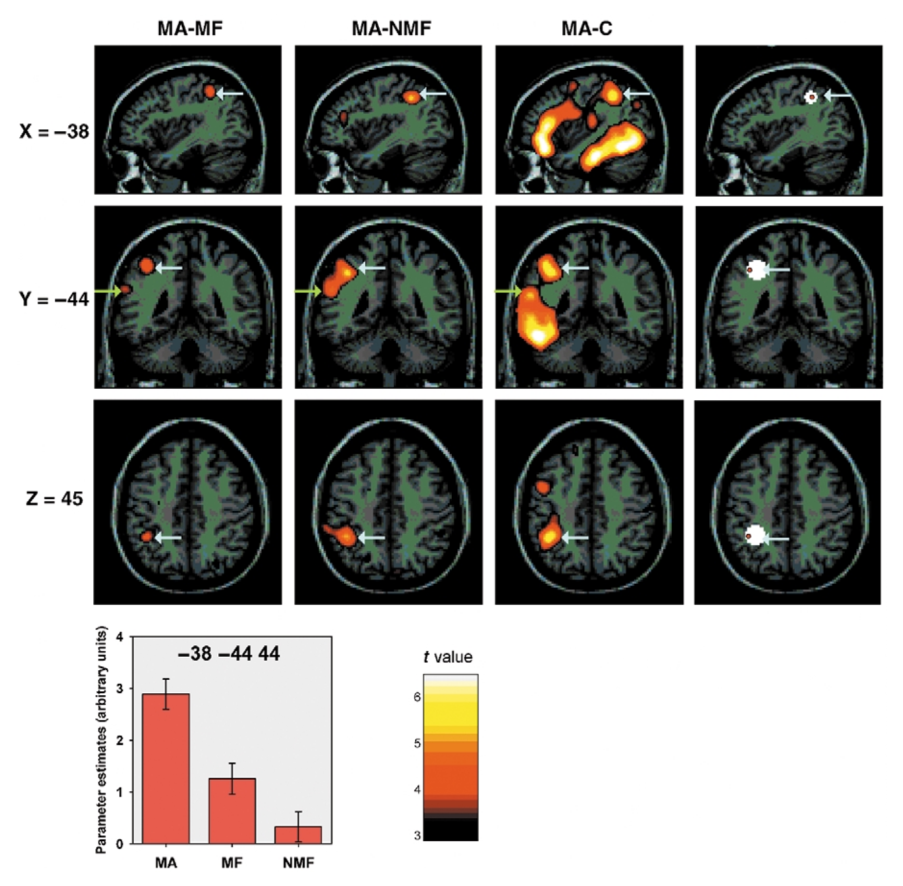

Figure 2. Attention mediated activation of the left inferior parietal lobule during semantic retrieval involving manipulable objects, i.e. tools. In contrast to left MTG and inferior frontal cortex that activate in response to the mere observation of tools, left BA40 (green arrows) and a location in the anterior intraparietal sulcus (blue arrows) show a marked sensitivity to the type of retrieval task. When performing action judgments in response to manipulable objects (MA), this region is more active than when making function judgments about manipulable objects (MF), function judgments about non-manipuable objects (NMF), or in a control condition that involved simply observing tools (C). The histogram illustrates the relative strength of the response within the point marked by the red dot within the parietal region of interest (white circles). Reproduced from [44] by permission of The MIT Press.

agnosic patient with bilateral temporal lobe lesions who had considerable difficulty identifying the functions of tools or the contexts in which they would typically be used. Nevertheless, he was capable of manipulating these items skillfully in a fashion appropriate with their usage [45]. This case might be interpreted as evidence for a non-semantic route between structural descriptions of objects constructed in earlier visual centers directly to parieto-frontal action representations. It is also possible that activation of semantic representations, insufficient for explicit recognition, is still capable of inducing automatic activation of action representations.

It is worth considering an alternative to the automatic activation of action representations during semantic tasks involving tools and/or actions. Perhaps activation of left parietal and premotor sites during semantic tasks involving tools indicates that they too play a role in representing *conceptual* information associated with these objects. More precisely, semantic information about tools might be distributed among several regions of the left hemisphere that are active at the time of encoding [46]. This seems reasonable if one assumes that visual properties of tools (involving left MTG) are likely to be acquired during active manipulation (involving sensori-motor regions of left parietal and premotor cortices). Conceivably, functional neuroimaging studies could be developed to distinguish between these two alternatives.

Overall, the neuroimaging results are generally consistent with a recent lesion analysis showing that patients with selective impairments performing non-verbal conceptual judgments about actions, including tool use, have maximal lesion overlap in a network of left-hemisphere regions including posterior left MTG, as well as premotor/prefrontal and parietal cortices [47].

Representing acquired tool-use skills

As early as 1905 (Liepmann, [17]), it was known that damage to the left PPC could affect the ability to produce skills associated with tools (Figure 1). In the intervening century there have been a variety of attempts to explain this fact [4]. One class of theories posit that Ideomotor Apraxia reflects damage to a more general faculty unique to the left hemisphere, such as the ability to construct symbolic representations (i.e. asymbolia) [48], or to form actions on the basis of objects' perceptual properties [49]. A second class argues that the posterior left hemisphere is the locus for representations of acquired tool-use skills. Specifically, Heilman and colleagues implicate the supramarginal gyrus, or Brodmann Area (BA) 40, of the left inferior parietal lobule. According to this view, Ideomotor

Apraxia resulting from damage to this region can therefore be understood as resulting from degradation of these motor memories [50].

Left parieto-frontal mechanisms and tool-use skills

A recent MRI-based lesion analysis reports that in comparison with left-hemisphere injured patients without apraxia, Ideomotor Apraxics present with maximal lesion overlap within and adjacent to the left intraparietal sulcus – including BA7, angular (BA 39) and supramarginal (BA 40) gyri – and/or the left middle frontal gyrus (GFm) [51]. To account for such observations, and behavioral differences between parietal and frontal-lesioned patients, Heilman and colleagues propose that these regions play different roles in representing tool-use skills [50]. Consistent with the idea that skill representations are damaged, patients with lesions including the left BA 40 have difficulty performing manual actions and discriminating 'good' versus 'bad' instances of observed actions. Patients with frontal lesions also perform poorly at production, but have no difficulties with action discrimination.

According to this view, intact discrimination indicates that patients with frontal lesions retain intact skill representations, yet have difficulty accessing this information for purposes of action production. This interpretation assumes that the same representations are involved in action production and recognition (see Box 2). This proposed distinction between the roles of frontal (retrieval) and parietal (representation) mechanisms in tool-use skills is well-suited for evaluation with functional neuroimaging techniques. However, in contrast to the sizeable literature on conceptual-level representations, few studies have used these methods to investigate mechanisms involved in representing and producing tool-use skills. Undoubtedly, the constraints of current neuroimaging techniques have contributed to this situation. Head movements, especially those correlated with task performance, can compromise the validity of fMRI results, and the workspace for limb movements is often highly constrained. Available studies to date have focused on pantomime, mental imagery, action observation, and the acquisition of skills associated with novel tools.

Consistent with the lesion-analysis data of Ideomotor Apraxics discussed above, Figure 3 illustrates that when activations associated with complex yet meaningless finger and limb movements are removed, pantomiming (Figure 3a) or imagining (3b) tool-use gestures with either hand activates left PPC in and around the intraparietal sulcus [52]. A similar pattern is also present when tool-use pantomimes involving either hand are contrasted with repetitive finger movements (Figure 3c) [53]. However, neither investigation observed activations in left GFm, as would be expected given the lesion-analysis data. Instead, they report left dorsolateral prefrontal [52] or dorsal premotor cortex [53] activations. One reason for these inconsistencies could have to do with experimental design. Both studies used block paradigms that assume that activations related to pantomime execution could be removed by subtracting data from non-gestural motor-control tasks. A limitation of this strategy is that any brain areas active in both the pantomime and motor-control conditions are eliminated. This could possibly be the fate of left GFm. The fact that the two studies differ from one another in terms of the left frontal areas they do find might reflect differences in the demands of their respective control tasks. Studies with more sophisticated experimental designs are needed before any strong conclusions can be advanced regarding the source(s) of differences between the lesion and neuroimaging data with regard to areas of left frontal cortex involved in representing tool-use skills. A crucial next step will involve using event-related and/or parametric designs to address outstanding issues like this one. For instance, is it possible to test Heilman *et al.*'s hypothesis about the differential roles of parietal and frontal mechanisms in skill representations? Likewise, studies of functional connectivity might enable neuroimagers to determine how and under what conditions brain regions in this left-lateralized network interact.

Another approach is to examine how brain areas respond to observation of tool-use actions. The validity of this approach for studying representations of skill depends on whether or not the same mechanisms contribute both to action comprehension and production, the so-called 'Common-Coding Hypothesis' [54,55]. By way of illustration, Johnson-Frey and colleagues found bilateral

Box 2. Toward a neural basis for the cultural transmission of tool-use skills

An important component of skill acquisition is the social exchange that occurs between people as new behaviors are taught and learned [67]. Recently, there has been considerable interest in identifying brain mechanisms that might enable us to form a link between observing others' actions and performing similar behaviors ourselves [68,69]. Much of this work is motivated by observations of mirror neurons in macaque inferior frontal cortex (area F5c) that respond either when the animal produces a given action or observes the experimenter performing a comparable behavior. Neuroimaging studies demonstrate similar responses in human left inferior frontal cortex (BA44), which might be a homologue of macaque area F5 [70]. With respect to tool use, it is important to note that these mirror cells' responses appear to depend on the animal observing [71] or inferring [72] specific interactions between the hand and target object. In other words, these neurons might represent observed goals of hand actions. Recent evidence indicates that human inferior frontal cortex also distinguishes between the goals inherent in observed hand–object interactions [56].

Inferior frontal cortex receives inputs from regions of the inferior parietal lobule implicated in the representation of object grasping and manipulation (anterior intraparietal cortex), and tool-use skills (supramarginal gyrus, or BA40; see Figure 4 in main text), as well as the superior temporal sulcus (STS). Perrett and colleagues describe cells in macaque anterior STS that code specific observed limb movements, and are sensitive to the direction of the actors' attention [73]. Like cells in F5c, some of these units are also sensitive to hand–object interactions [74]. Likewise, Iacoboni and colleagues recently presented evidence that a region in the human STS is involved in matching observed actions with those being produced during imitation [75]. Together these sources of evidence suggest the existence of a distributed representational system for bridging between the perception and production of action [54,55]. This circuit has characteristics that could serve as a critical mechanism for the cultural transmission of skills including tool use in humans through observational learning and/or imitation. The relationship between this system and those involved in representing semantic knowledge about tools and tool-use skills is a topic in need of investigation.

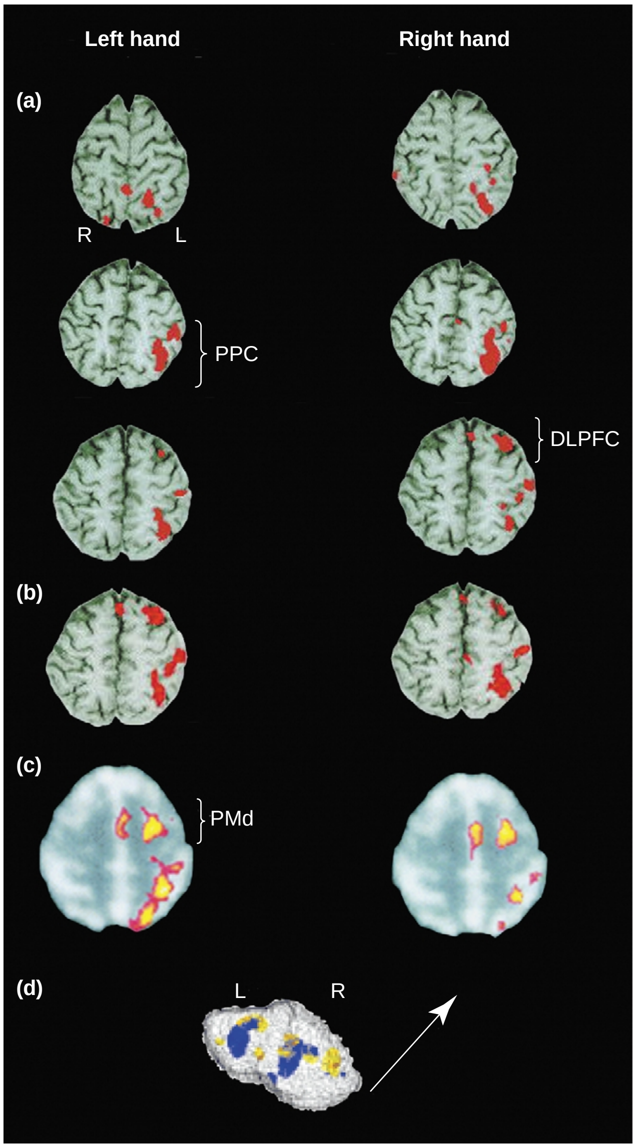

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Figure 3. Brain regions activated during production of tool-use pantomimes and actions. (Note that in panels a–c, the brain is shown in radiological coordinates, i.e. the left hemisphere is displayed on the right side and vice versa). **(a)** Activations in three subjects associated with pantomime production after subtracting activity related to finger and limb movements [52]. Activity is highly lateralized to the left parietal and frontal cortices, and there is a high degree of similarity within subjects when pantomimes are produced with either the left or right hand. Both activate left posterior parietal cortex (PPC) and dorsolateral prefrontal cortex (DLPFC). **(b)** A similar pattern is observed when the third case from Panel A imagines producing tool-use pantomimes [52]. **(c)** Left parieto-frontal activity is also observed when pantomime production is contrasted with repetitive finger movements [53], but frontal activity is more posterior in dorsal premotor cortex (PMd). (See text for discussion of this difference.) This study also observed bilateral activity in cerebellum. **(d)** 3-D surface reconstruction of the cerebellum with functional overlay as viewed from a superior-posterior-lateral perspective [58]. The white arrow indicates the anterior–posterior axis, pointing in the anterior direction. Areas whose activity is correlated with manipulating specific types of novel tools (computer mice with different input–output properties) appear to cluster together. Activity in blue-white areas is correlated with manipulating a mouse with transformed velocity vs. a normal mouse (blue = highest correlation); orange-yellow areas with manipulating a mouse that has undergone a rotational transformation vs. a normal mouse (orange = highest correlation).

responses in inferior frontal cortex when subjects observed static images of tools and other objects being grasped versus incidentally touched. However, these responses did not depend on whether the objects were tools or unfamiliar shapes, or whether the tools were being grasped in a familiar versus unfamiliar fashion [56]. Further work looking at the whole brain during observation of dynamic tool-use actions is needed.

Finally, Imamizu *et al.* have investigated changes in brain activation associated with learning to use a familiar tool that behaves uncharacteristically; that is, a computer mouse whose movements had consequences for a cursor that had undergone rotational transformations [57,58]. These findings indicate that as the skill of using the mouse is mastered (actually re-mastered), there is an increase within a localized sector of the cerebellum (posterior superior fissure) that might reflect the construction of an internal model of the new tool-use skill (Figure 3d) [57]. Subsequent work shows that when subjects acquire skills with two mice having different input-output mappings, separate locations in the cerebellum show increased activity, suggesting that skills associated with each tool might be localized to distinct cerebellar regions [58]. This work raises several interesting questions concerning the relationship between the cerebellum and cerebral cortex in the acquisition and representation of tool-use skills. If the cerebellum stores representations of tool-use skills then why don't cerebellar lesions cause Ideomotor Apraxia? Is the cerebellum only important for the acquisition of new tool-use skills, with long-term representations being supported at the cortical level? It would be extremely useful to know what sorts of changes in brain activity are taking place in posterior parietal and/or frontal regions during the acquisition of tool-use skills such as these. Here too analyses of functional connectivity could prove useful in deciphering complex interactions across multiple brain regions (see also Box 3 for other outstanding research questions).

Conclusions

Our understanding of the neural bases of human tool use owes much to the observations of those who have studied behavioral deficits following brain injuries over the past 100 or more years (see also [59], in this issue). Indeed, as observed by early investigators, separate regions in the human left hemisphere are involved in representing conceptual knowledge concerning tools and their associated actions versus the acquired skills involved in their

Box 3. Questions for future research

- What specific evolutionary changes in primate brain organization account for the evolution of complex tool use in humans?
- What is the relationship between left-hemisphere systems responsible for complex human tool use and language?
- What systems are involved in acquiring conceptual knowledge about tools versus skills involved in their usage?
- How does tool-use expertise affect the way that semantic knowledge about tools and their uses are represented?
- What brain mechanisms are involved in the planning and manufacture of novel tools?
- Can the development of tool-use skills during childhood be related to changes in specific brain mechanisms?
- What is the relationship between representations of tool-use skills and other acquired manual behaviors that do not involve objects (e.g. waving goodbye).

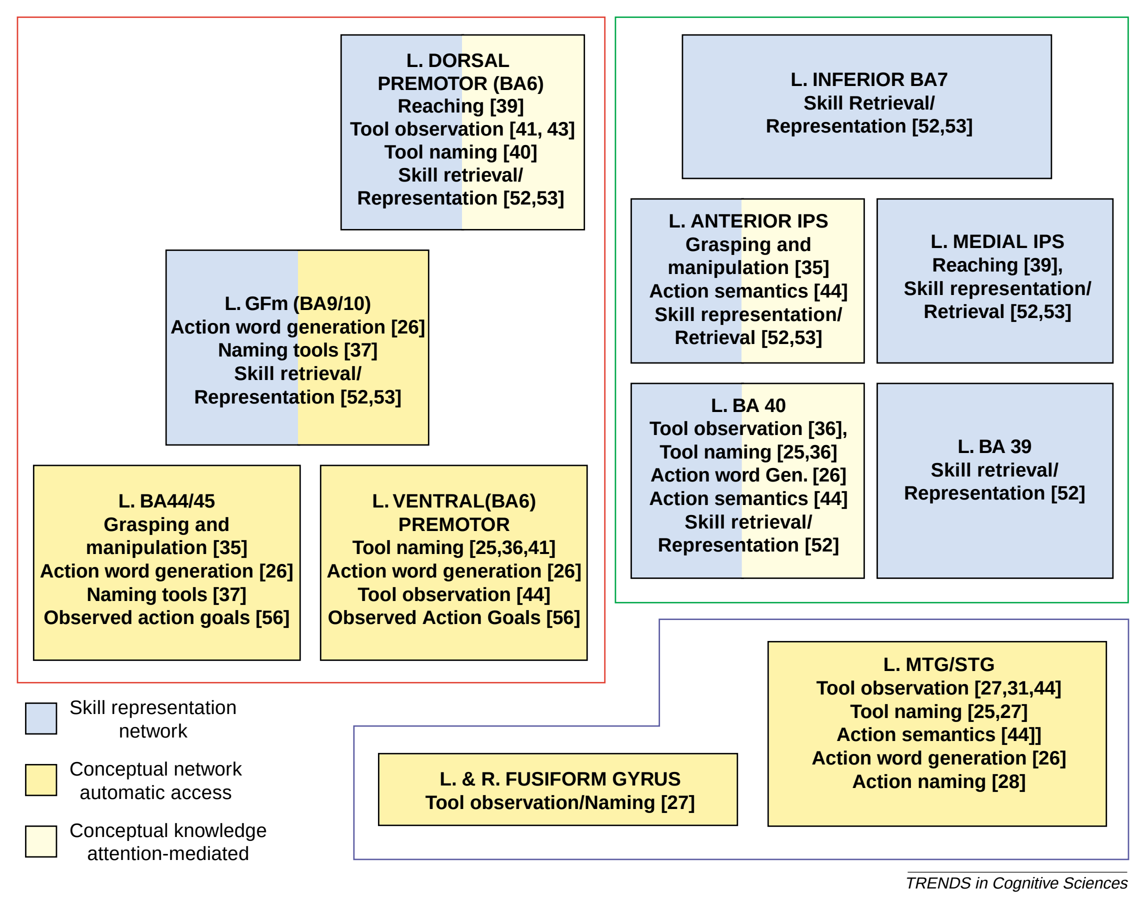

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Figure 4. A schematic diagram depicting two distributed networks in the left cerebral hemisphere hypothesized to support complex human tool use. Conceptual network (yellow): areas known to be activated during semantic tasks involving tools and/or associated actions.Skill network (blue): areas known to be activated during retrieval of tool-use skills. Areas colored both blue and yellow are known to be activated during semantic and skill-production tasks, possibly as a result of automatic activation of action representations during semantic access. Activations during semantic tasks in three of these regions (indicated by pale yellow) might be mediated by attention demands of the tasks. Larger outlines indicate the lobes to which these areas belong: parietal (green), frontal (red), and temporal (blue). See text for details.

usage (Figure 1). These insights have been refined by functional neuroimaging studies demonstrating that these areas are components of widely distributed, yet highly interactive, networks involving not only parietal, but also temporal and frontal cortices (summarized by Figure 4). These advances demonstrate the utility of seeking convergent validation between behavioral investigations of lesion patients and functional neuroimaging when seeking to understand complex, real-world behaviors.

Acknowledgements

Scott H. Johnson-Frey was formerly known as Scott H. Johnson. Preparation of this manuscript was supported by grants from NIMH (#MH002022–02) and the James S. McDonnell Foundation. This manuscript benefited from the constructive criticisms of the anonymous reviewers, and Valerie Gerry.

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