What's So Special about Human Tool Use?

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Evidence suggests homologies in parietofrontal circuits involved in object prehension among humans and monkeys. Likewise, tool use is known to induce functional reorganization of their visuotactile limb representations. Yet, humans are the only species for whom tool use is a defining and universal characteristic. Why? Comparative studies of chimpanzee tool use indicate that critical differences are likely to be found in mechanisms involved in causal reasoning rather than those implementing sensorimotor transformations. Available evidence implicates higher-level perceptual areas in these processes.

Interacting manually with objects in the environment poses considerable challenges for the sensorimotor systems of primates. Electrophysiological studies of nonhuman primates suggest that these problems are solved by functionally specialized parietofrontal circuits that transform sensory representations of the body and the surrounding environment into motor plans for prehension (reaching, grasping, and manipulation of objects). The efficiency of these solutions is attested to by the universality of dexterous prehension among primates.

Tool use introduces a new set of difficulties. The physical characteristics of the tool, its relationship to the body and to the surrounding environment all impinge upon its effective utilization. While many species dexterously use simple tools to solve problems in their environments, the ability of even our closest living relative, the chimpanzee, to solve environmental challenges through tool use pales in comparison to that of young children. With growing evidence for homologies among primates in parietofrontal circuits that control prehension, the obvious question is why?

Homologous Parietofrontal Systems for Prehension

As summarized in Figure 1, electrophysiological studies of macaques reveal the existence of parietofrontal circuits that are involved in sensory-guided prehension. The precise computations implemented within these circuits are a source of ongoing research and debate that exceed the scope of this review (see Andersen and Buneo, 2002; Marconi et al., 2001; Rizzolatti and Luppino, 2001). Nevertheless, parietofrontal circuits involved in reaching, grasping, and object manipulation have been distinguished, and a growing body of evidence from functional neuroimaging points to the existence of ho-

mologous circuits in humans (e.g., Culham and Kanwisher, 2001).

Reach System. 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. In macaques, these transformations are accomplished within a circuit interconnecting one or more regions located within the medial intraparietal sulcus (IPS) and dorsal premotor cortex (PMd) (Andersen and Buneo, 2002; Johnson et al., 1996). Area PMd is well situated for computing premovement plans for reaching. It receives direct visual and higher-level proprioceptive input from the superior parietal lobule (SPL). Likewise, somatosensory information concerning limb position is provided to PMd via a circuit interconnecting PEc/PEip-F2. This sensory input is integrated within PMd neurons to form plans for using a particular limb to reach to a specific target location (Hoshi and Tanji, 2000). Evidence for a "reach" circuit in humans involving putative homologs of medial intraparietal cortex and PMd has recently been reported (Johnson et al., 2002).

Grasp System. Grasping involves integrating representations of objects' intrinsic spatial properties (e.g., shape, size, texture) with properties of the hand and fingers. In the macaques, this is accomplished in a more ventral parietofrontal circuit connecting the anterior intraparietal area (AIP) and area F5 located in ventral premotor cortex (PMv) (Sakata et al., 1997). Area AIP contains several subpopulations of "manipulation" cells that represent specific types of hand postures necessary for grasping objects of differing shapes. Area F5ab receives a major projection from AIP, and cells appear to represent specific manual actions (Rizzolatti et al., 2002). In humans, significant activation within the anterior IPS (putative AIP) and inferior frontal cortex is observed when objects are grasped (Binkofski et al., 1999), and lesions in this circuit produce deficits in configuring the hand to engage objects effectively (Binkofski et al., 1998).

Manipulation System. Visuotactile representations of peripersonal space centered on the body part involved in a given visually guided action, such as object manipulation, are constructed in a circuit connecting the ventral intraparietal area (VIP) with area F4 in PMv (Graziano and Gross, 1998) (Figure 1). The majority of units in F4 are bimodal, having tactile receptive fields (RFs) that are in register with 3D visual RFs of space immediately adjacent to the animal. Similar RF properties are found in VIP and in cells distributed throughout the IPS. What is special about these units is that their receptive field properties are altered by tool use. Specifically, as shown in Figure 2, visual RFs *expand* when monkeys use a rake to retrieve other objects (i.e., food pellets; Iriki et al., 1996). Visual RFs normally in register with tactile RFs of the hand now encompass peripersonal space occupied by the rake. Importantly, such expansion is not observed when monkeys unsuccessfully attempt to retrieve food with an ineffective manipulandum (Figure 2). Therefore the increase in the representation of peripersonal space

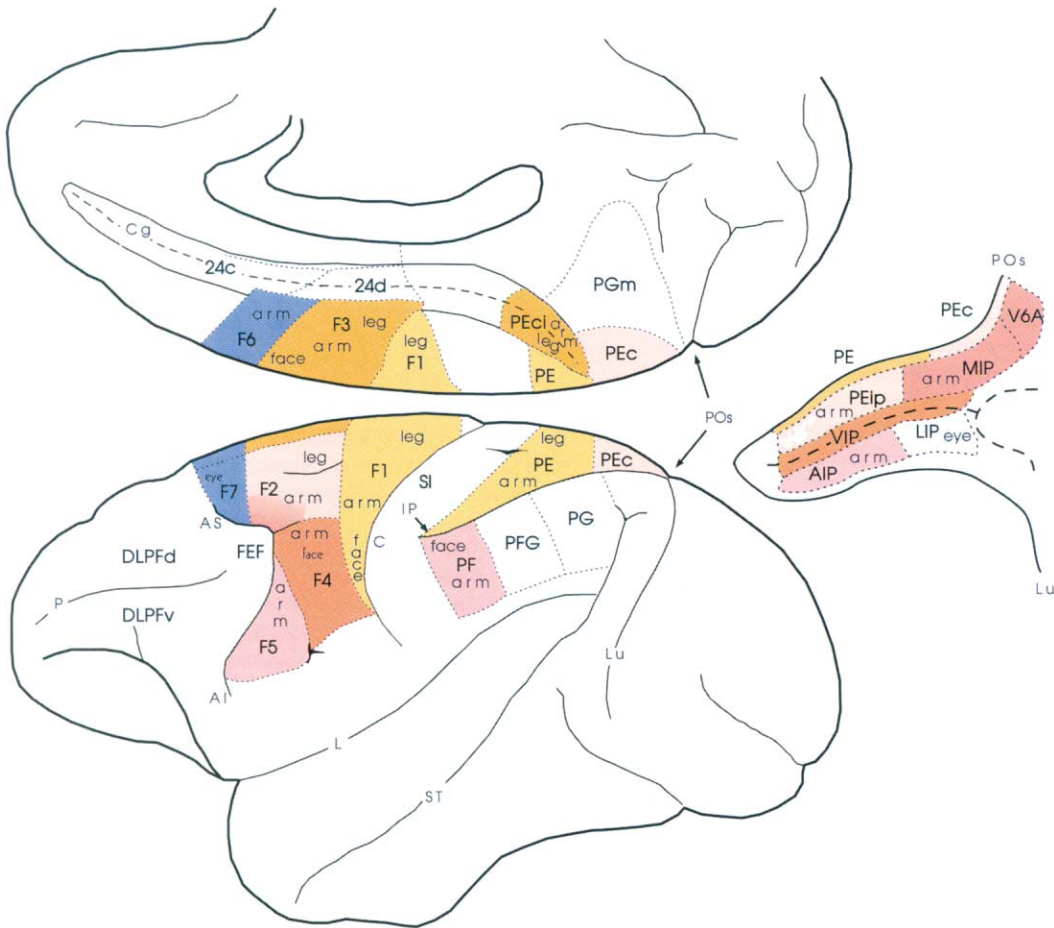*Correspondence: scott.h.johnson@dartmouth.edu

Figure 1. Parietofrontal Areas Involved in Sensorimotor Transformations

Parietal and frontal areas that are interconnected are shown in the common colors. Blue denotes areas receiving input from prefrontal cortex. (A) Parcellation of the motor, posterior parietal, and cingulate cortices displayed on mesial and lateral surfaces of a macaque brain. (B) The intraparietal sulcus unfolded to reveal functionally defined areas. Adapted by permission from Rizzolatti and Luppino (2001).

depends on whether a manipulandum is used to achieve an intended goal (Obayashi et al., 2001).

Similarly, using tongs that extend the reach versus fingers to manipulate small objects is associated with increased activation in the ipsilateral IPS in humans (Inoue et al., 2001). Moreover, patients with parietal lesions demonstrate behavioral effects that nicely compliment the single unit data from macaques. For instance, a right parietal damaged patient with unilateral left-neglect evidences the expected right-bias when asked to bisect a horizontal line in near space. The patient performs normally when bisecting lines located beyond peripersonal space with a laser pointer. Interestingly, when bisecting distant lines with a handheld stick, left-neglect is again evident. Similar to expansions of visuotactile RFs in IPS neurons, use of a tool causes distant space to be remapped as "within reach," leading to a neglect-related bias in performance (Berti and Frassinetti, 2000).

Parietofrontal circuits involved in reach, grasp, and object manipulation undoubtedly form the foundation upon which more complex tool use behaviors rest. Yet, the void between here and understanding the mechanisms responsible for even the average 2-year-old child's tool use repertoire is expansive. Comparative

studies of our nearest living relatives, chimpanzees, suggest that processes involved in reasoning about objects' physical properties and causal interactions may hold the key to complex tool use behaviors.

Comparative Studies of Tool Use in Chimpanzees
Amid growing evidence for homologous mechanisms involved in the control of prehension among primates, one might not expect profound differences between humans and chimpanzees in the capacity for tool use. Unlike macaques, chimpanzees are well known to use and even manufacture tools in the wild, and classic experiments by Köhler long ago demonstrated that they are capable of using objects to solve sophisticated problems. Yet, a series of elegant studies by Daniel Povinelli and colleagues reveals heretofore overlooked limitations on the ability of chimpanzees to solve tool use problems that are surprisingly simple from a human perspective (Povinelli, 2000). Keeping with the discussion above, consider the ability to use a rake to retrieve a food item. Chimps have no difficulties with this task in its modal form. They likewise perform well when asked to choose between pulling a rake with an intact handle versus one with a clearly broken handle, as illustrated in Figure 3A. But does this indicate that they appreciate
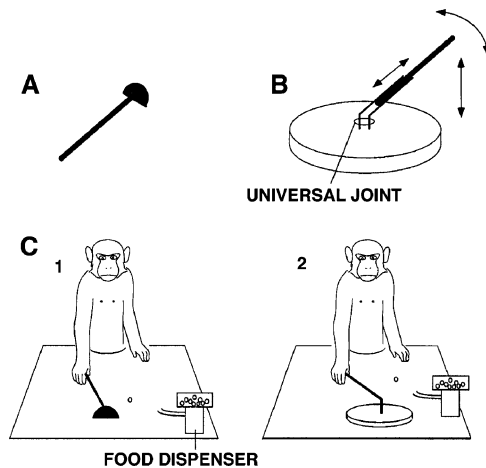
Figure 2. Apparatus and Task Used to Investigate Neural Mechanisms of Tool Use in Macaques

(A) A rake that could be used as a tool to successfully capture and retrieve food pellets. (B) A control manipulandum that connects a rake handle to a universal joint making it impossible to successfully retrieve food pellets. (C) The experimental (1) and control (2) conditions in which the monkey attempted to retrieve food pellets with the rake or manipulandum. By comparing brain activation in these two conditions, it is possible to separate mechanisms involved in tool use from areas contributing to object manipulation. Adapted by permission from Obayashi et al. (2001).
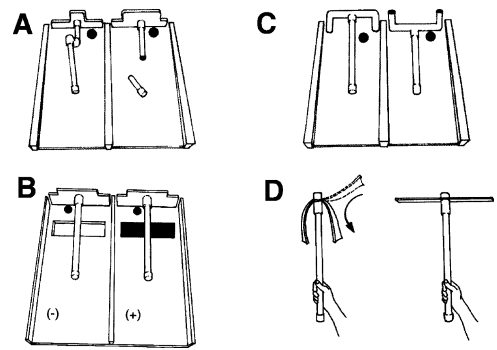

Figure 3. Four Tasks Used by Povinelli and Colleagues to Investigate Causal Reasoning by Chimpanzees in the Context of Tool Use

In all tasks, the goal was to pull the rake that would successfully bring a food item within reach. (A) The broken-rake problem in which chimpanzees were required to choose between an intact rake and one with a clearly broken handle. This was accomplished with minimal difficulty. (B) The table-trap problem in which the choice was between pulling a rake that would cause the food item to fall into a well (left) or one in which the food item would be successfully obtained (right). Note that the rectangle on the right side of the table was painted to maintain perceptual similarity. However, it was clearly distinguishable from the 3D well on the left side. (C) The inverted-rake problem where chimpanzees were asked to chose between a rake, an upright rake, and one that had been inverted, making it ineffective for capturing food. (D) The flimsy-tool problem wherein chimpanzees had to select either a rigid rake or an ineffective one made of nonrigid rubber. As detailed in the text, tasks B, C, and D proved difficult for chimpanzees to solve. Adapted by permission from Povinelli (2000).

the causal relationships between self, tool, and goal object? Their failure on seemingly simple modifications of this and numerous other paradigms suggests that they do not. For instance, adult animals averaged only slightly better than chance when given the choice between pulling a rake in the modal condition versus one in which the food would, from our perspective, obviously fall into a well before being pulled to within reach (Figure 3B). If given the choice between pulling a modal rake versus one in which the rake was inverted so as to be "obviously" ineffective, they were no better than chance (Figure 3C). Chimpanzees were also at chance when asked to choose between the modal rake and one modified such that the tines were constructed of flimsy rubber that could not possibly capture the goal object (Figure 3D). How can these inconsistencies be explained?

Consistent with the putative homologies reviewed above, Povinelli argues that apparent similarities in the overt behaviors of humans and chimpanzees, including some aspects of tool use, may be attributed to the fact that both species draw on common sensorimotor abilities. However, what these studies reveal is that chimpanzees differ profoundly from humans in their understanding of the abstract causal variables that govern objects and their relationships in the physical world; an understanding that begins to emerge during early infancy in humans (Spelke et al., 1992). As a consequence, they often fail at tasks that demand using an internal model of causal relationships to *anticipate* which of two actions will result in the desired consequences.

The major implication of these findings is that neuroscientists interested in mechanisms responsible for complex tool use might do well to direct their efforts toward identifying and interrogating brain regions involved in reasoning about objects' physical properties and causal relationships.

Neural Mechanisms of Causal Reasoning

To date there are remarkably little data concerning the neural bases of processes required to understand physical causality of the sort necessary for complex tool use. On the one hand, it has long been known that patients with frontal/prefrontal injuries are impaired on tasks that demand planning and executing complex goal-oriented actions (Shallice, 1982). More recently, functional neuroimaging studies have provided convergent evidence for the involvement of frontal/prefrontal areas in these processes (Fincham et al., 2002). On the other hand, as I will point out below, the available data suggest that these regions may not be critical to understanding physical causality. Instead, internal models of objects' physical properties and causal relationships may be constructed in areas of temporal and/or parietal cortex associated with higher-level perceptual processing.

Causal relationships between hands and other objects appear to be coded in the temporal cortex of monkeys. Cells within the lower bank of the superior temporal sulcus (STS, area TEa) respond selectively to the observation of movements of objects caused by hands (Perrett et al., 1990). Responses are reduced when objects and hands move congruently but without making physical contact. Similarly, observing one ball contact and launch another versus launching in the absence of contact is associated with bilateral activity within the human STS and left IPS (Blakemore et al., 2001).

Neuropsychological evidence also indicates that parietal and/or temporal cortex are critical to reasoning
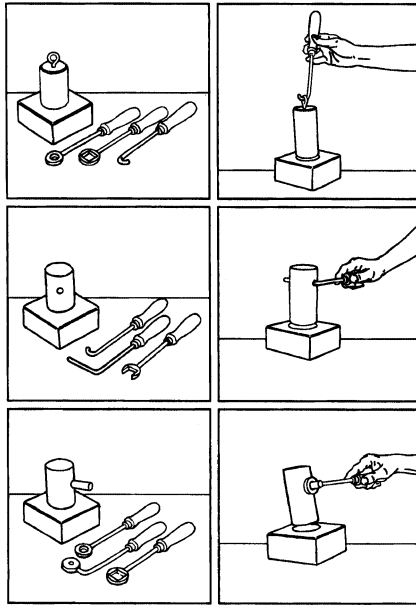
Figure 4. Three Novel Tool Selection Tasks Used by Goldenberg and Hagmann

The left-hand column shows the three alternative tools and the one goal object, while the column on the right illustrates the correct solutions to the mechanical reasoning problems. Adapted by permission from Goldenberg and Hagmann (1998).

about causal relationships involving tools and goal objects, particularly in the left cerebral hemisphere. As depicted in Figure 4, Goldenberg and Hagmann (1998) show that left brain-injured patients are impaired (79.2% correct) at selecting a novel tool to perform a particular task solely on the basis of its physical properties, whereas individuals with right hemisphere lesions (96.6%) do not differ significantly from age-matched controls (100%). Importantly, lesion analyses indicate that frontal lobe damage did not affect performance. By contrast, only 19% of patients with parietal injuries and 34% with temporal lobe damage were successful in selecting task-appropriate tools.

Causal reasoning in tool use does not, however, depend on the same perceptual mechanisms as object recognition. Patients with semantic dementia due to focal atrophy of temporal cortex have considerable difficulty identifying common objects and their associated functions yet are known to perform well on the novel tool task (Hodges et al., 1999). This is not simply due to differences in task difficulty, as the opposite pattern of intact object recognition with impaired novel tool selection occurs with bilateral parietal atrophy related to corticobasal degeneration (Spatt et al., 2002).

More work is clearly needed to understand better the neural substrates involved in causal reasoning and tool use. Though limited, currently available data implicate higher-level temporal cortex in processing causal interactions between external physical objects, while reasoning about the uses of unfamiliar tools appears to depend on parietal and/or joint parietotemporal mechanisms.

Conclusions

So, what is special about human tool use? Though far from definitive, clues from several relatively isolated do-

mains suggest that the answer may lie in understanding how the human brain represents physical causality. Hopefully, this review will stimulate further explorations of this fundamental question that to date has been relatively overlooked by neuroscience.

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