The neural origins and implications of imitation, mirror neurons and tool use
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Several recent studies report how laboratory-raised, non-human primates exposed to tool use can exhibit intelligent behaviors, such as imitation and reference vocal control, that are never seen in their wild counterparts. Tool-use training appears to forge a novel cortico-cortical connection that underlies this boost in capacity, which normally exists only as latent potential in lower primates. Although tool-use training is patently non-naturalistic, its marked effects on brain organization and behavior could shed light on the evolution of higher intelligence in humans.

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Introduction
‘Civilized’ behavior dictates the ways in which people are expected to speak, emote and move. The rules for movement are interesting, as they often impose highly ornate components on otherwise utilitarian motor sequences. For examples, one needs to look no further than the formal dining etiquette of utensil usage. These ‘refinements’ to the movements of diners do not practically enhance the act of eating, and can even make it physically awkward. Such culturally imposed ‘good manners’ are especially prevalent when it comes to instruments or tools. Perhaps this is because tools explicitly manifest the movements of the body parts using them or, alternatively, because tools are objectified as extensions of the body.

Uncouth action, even if competent to achieve a goal, is frowned upon — perhaps because it seems animalistic. The actions of animals in the wild are driven by immediate necessity, which is imposed either externally, by the environment, or internally, by emotion. In human terms, their behavior is uninhibited, unselfconscious and unrefined. Non-human animals cannot imitate the pure form of an action, because their actions are inseparable from the driving conditions.

Humans, by contrast, can perceive, imitate and transmit the form of an action independently of its goal or other driving factors. This trait is fundamental to culture and civilization. It also constrains or guides many of our actions as we strive to conform to the rules of civilized behavior and to avoid negative judgment from other members of society.

Here, I propose that a set of neuronal adaptations that arose during hominid evolution have endowed us with this uniquely advanced capacity for refined movement. I also propose that tool-use training can elicit similar, if lesser, imitative capabilities in lower primates, which could open a new horizon for behavioral, cognitive and social primate neuroscience.

Puzzles of monkey imitation and tool-use
In human society, cultural knowledge is propagated and shared through mutual imitation (see glossary). The mirror neuron system (see glossary; neural substrates that are activated equally during the execution and observation of any given goal-directed action) is widely assumed to subserve this human faculty (outlined as blue circuitry in Figure 1)[1,2,3].

Mirror neurons were originally discovered in the monkey brain, first in the premotor cortex [4], and later in the areas around the intraparietal sulcus (IPS) [5,6]. In addition, a similar group of neurons that responds to biological motions (see glossary) exists in the supratemporal sulcus (STS) [7,8]. Thus, monkeys are able to sense the goals, not just the movements, of other agents’ actions. And yet despite this, puzzlingly, non-human primates in the wild do not imitate the actions of others [9].

However, recent studies report that some primates can develop efficient tool-use skills through social learning [10–12]. Also, macaque monkeys can imitate cognitive, but not action, tasks [13]; can recognize when they are being imitated even though they cannot normally imitate [14]; can imitate once joint attention is established [15]; and can attribute perception to others [16]. Thus, the fundamental imitative mechanisms apparently exist in lower primates, but under ecological conditions they do not give rise to volitional imitation. However, they do seem to give monkeys a latent capacity for imitation, which tool-use training can amplify to a degree that emerges in behavior.
What, then, is special about tool-use? Tools are hand-held objects used to manipulate secondary objects. Tools are assimilated into the body schema (see glossary) and perceived as externalized hands in humans — a process that is probably subserved by the same neural mechanisms that have been described in monkey intraparietal bimodal (visuo-tactile) neurons (see glossary) [17]. Alternatively, hands could have become objectified — perceived as just another kind of tool — and, as such, could provide a means to explicitly perceive, manipulate and imitate action ‘objects’ that are divorced from their goals or motivations. In the following sections, I sketch a proposal for how these adaptations have been implemented in the neural circuitry of the primate brain.

Neural systems for social mirroring
Mirror neurons discharge equally (and continuously) while a monkey performs a goal-directed action and while it watches another agent perform an equivalent action [4]. To aid our understanding of what these neurons are doing, we can consider the problem to be composed of three components: first, the environmentally or emotionally derived goal that elicits a behavior, which can also be thought of as the intention or a ‘drive’ to fulfill such a goal; second, the form of the behavior or action itself; third, either the agent performing the behavior or the one observing it.

Glossary
Autistic spectrum disorder: Autistic patients have difficulty empathizing with the mental and emotional states of others, and imitating their actions. They also tend to persist in restricted and repetitive patterns of behaviors. As the word ‘spectrum’ implies, the resulting social impairment can range from minor to total, depending on the severity of the condition.

Biological motion: Relational patterns of movement among abstract elements, such as ensemble of dots, that nonetheless evoke a strong perception of a moving animal or human. These patterns are extracted by specialized neurons in the superior temporal sulcus.

Body schema: Knowledge or information about the configuration, posture, location and movement of the body in space, together with assessments of the anatomical and functional relationships of different body parts. This information is postulated to be composed by multisensory (particularly somatosensory and visual) integration related to the body in space, and is formed and stored in the parietal cortex.

Canonical neurons: Neurons in macaque monkey premotor cortex that become active when a monkey grasps or views a graspable object. Thus, the visual features of the object, in relation to its affordance properties (how it can be held, used and manipulated), seem to contribute to the encoding of the motor sequence needed to grasp it.

Imitation: The replication of the behavior of one agent by another. It is important to distinguish ‘true imitation’ from mere example-following. In true imitation, the pure form of an action is replicated, independent of its drive or intent; in example-following, (i.e. stimulus, local and social enhancement, and goal emulation), one animal adopts the same goal as another but does not replicate its movements in detail, rather, just evoking similar movements from observer’s existing repertoire.

Intraparietal bimodal neurons: In monkeys trained to use a rake as an extension of the hand, we found that the receptive field properties of intraparietal bimodal (somatosensory and visual) neurons represented assimilation of the tool into the body schema. That is, their visual receptive fields, normally located around the hand to encompass their tactile receptive fields, extended to include the length of the rake, as long as the monkey intended to use it as a tool.

Magnopyramidal neurons: Very large pyramidal neurons in the human cerebral cortex, the functions of which are not fully understood. This includes those revealed by lipofuscin stains detected particularly in thick (400–1000 μm) sections by low-power pigmentoarchitectonic examinations, or acetylcholinesterase-rich pyramidal neurons.

Mirror neurons (cf. mirror neuron system): Neurons found in macaque premotor cortex that are activated equally during the execution of any given goal-directed action and during observation of equivalent actions by others, thus ‘mirroring’ the actions of self and others. Similar patterns of brain activations have been detected in humans through brain imaging, but no direct, single-unit neuronal discharges have been recorded to date. Thus, they are usually referred to collectively as the ‘mirror neuron system.’

Reference call (cf. emotional call): Reference calls are voluntarily emitted, arbitrary forms of vocalization, used to indicate or refer to specific objects or events. This is in contrast to ordinary forms of animal vocalization, or emotional calls, which are involuntarily triggered in reaction to external stimuli.

Somatic marker: A hypothesized link between intellectual and emotional events in the mind and body, especially visceral, reactive experiences — a notion captured by the phrase ‘gut feeling’. Thus, the representation by the brain of its emotional state is strongly coupled to bodily sensation.

Theory of mind: The ability to read and estimate the mental states of other agents. Mental states can include intention, emotion, disposition, desire, beliefs and so on, which in turn determine the upcoming actions of agents. This ability is thought to be unique to humans, except that only a very primitive form is seen in apes.
Mirror neuron discharge is coupled to the immediate goal of the action but is ‘blind’ to the details of its form. The environment supplies (as a cause of action) both the goal and the object that must be acted upon to achieve it. Indeed, the mirror neurons of the intraparietal lobule discharge differently to identical motor actions depending on the meaning of the action in context [6**]. Conversely, identical mirror neuron activity occurs when observing and executing different actions that have the same goal [5]. Canonical neurons (see glossary) that co-reside with mirror neurons in the premotor cortex discharge when a monkey sees an object to grasp [18], and a group of neurons in the anterior intraparietal area have similar visual properties to code grasping actions [19,20]. Auditory mirror neurons fire when a monkey hears the sounds related to the actions to which they are attuned [21]. Tool-responding mirror neurons enable the monkeys (who are unable to use tools) to extend their capacity to understand the goal of tool-using actions by the experimenter, which do not correspond to existing action repertoires of the monkeys [22]. These discharges represent the causes and expected effect of the actions they encode.

Thus, the activity of a mirror neuron is coupled to the immediate goal of action but is ‘blind’ to the details of its form. Lyons et al. [23] assumed, somewhat similarly, that mirror neuron activity encodes a concise representation of just the final goal of an action by ‘intentional compression’ rather than by encoding the detailed features of subgoals of action sequences. The human mirror neuron system also functions to grasp the intention of others [2], in addition to extracting the forms of actions.

Thus, the mirror neuron system should contribute to the selection of actions for immediate execution on the basis of current social environmental conditions (shown as the blue square on the left of Figure 2). This action-readying can come about either through direct interaction with the environment or through action observation — namely, social mirroring. In these situations, actions can only be induced externally, and their forms will be entirely dictated by immediately extant conditions. Hence, true imitation — a copy of the form of an action independent of agency and actual goal — is not possible.

Similar mechanisms for mirroring emotions on the basis of facial expressions have been identified in human brain imaging studies [24–27]. There is an affective mirror neuron system that includes the insula, amygdala, limbic system and STS — in the STS, the affective mirror system is interfaced with the action mirroring system described above [28] (shown as orange systems in Figure 1). Mirror neuron discharge in this system represents a nexus of emotional drive and forms of facial expression or body language of the agent. Here, the nexus underlies the sharing of emotional expressions, in addition to the emotions themselves, among members of society (shown as the orange square on the left of Figure 2).

But unlike the action system, emotion does not induce, by itself, direct effects on the environment: there is no object to manipulate. In addition, humans are not in full control of their emotions in the way that they are of their actions. Hence, we cannot truly relive each other’s emotion, and in this respect we resemble non-human primates, who are unable to truly imitate actions.

**Self-objectification through tool-use learning**

In addition to the largely environmentally driven action system of animals, humans seem to possess a genuinely voluntary intention system that can perform, or even just imagine, actions divorced from immediate context. This system not only enables us to mirror and understand the intentions of other people, it endows us with a fully developed theory of mind (see glossary) [29,30]. The medial prefrontal cortex (MPFC), temporoparietal junction (TPJ, especially right hemisphere in humans) and temporal pole, together with a few additional structures, might carry out this function [29,31**–32] (depicted in green circuitry in Figure 1).

Non-human primates show, to date, no sign of this kind of sense of the subjective self. But we have recently discovered that in monkeys, significant intracortical connections between the intraparietal cortex (IPS) and the TPJ can be forged by tool-use learning (shown as the red line in Figure 1) [33**]. The IPS is a part of the mirror neuron system (Figure 1, blue), and has neurons that, after tool-use, encode a modified body schema [17]. When the TPJ is damaged or stimulated in human patients, they occasionally experience unusual feelings of ‘autoscopy’ or ‘out-of-body experience’, that is, an illusion of observing themselves from a third-person point of view [34,35*]. The subjective self is relocated outside the body and the body is objectified; it becomes a thing in the environment that could be manipulated.

How can tool-use learning drive interactions between the TPJ and the IPS? One potential explanation is that use of the tool as an extension of innate body parts induces a temporary mismatch with an existing body image stored in the IPS region, and thus requires recalibration that is driven by the monkey’s own intention to incorporate the external object (tool) into its internal body self-representation. Thus, tool-use training could have brought about explicit awareness of the monkey’s own body and own intentions (or mind), and eventually induced neural connections subserving it. Thanks to these newly formed ‘TPJ–IPS connections, the subject can objectify its body parts as equivalent to external tools. Now from the tightly coupled nexus of the actions’ causal structure, the sense of the agent has split into ‘subjective self’ and ‘objective self-body’ (shown as bifurcating green
arrows in Figure 2) to form an internal causal cascade (Figure 2, right diagram).

Thus, forms of action can be explicitly and independently represented. This kind of mind–body linkage, viewing the ‘self’ as consisting of several component mental processes and body parts [36], would not merely be induced within the tool user. Tools can be used in identical ways for identical purposes by both self and others. Hence, tools could be a medium for realizing equivalence among agents and of self–other compatibility. Thus, tool-use induced TPJ–IPS connections could form a crucial bridge between the mirror system and a mental state attributor, enabling imitation of each other’s forms of actions.

Recently, laboratory-raised bonobos and orangutans were reported to save the tool aside for future use [37], a behavior that is never seen in wild habitats [38]. This behavior could be subserved by a sense of the subjective self, continuous and lasting over time, which could have emerged through the abundant, daily tool use to which the house-raised apes were exposed.

**Structure of human and non-human actions**

Efficiency and grace often matter greatly in human actions. People often pay attention to the forms of their actions, because we can design them and modify them according to the environment, social context, or conscious choice. This is most evident when augmenting human action with tools or machinery, at which point the purpose of the action must be pre-determined and its form must be explicitly tailored to its goal.

The left half of Figure 2 represents the mirror system of animals, in which the form and the agent of actions are
inseparable and environmentally driven. The right part of Figure 2 depicts the structure of the human action system, in which subject and object are separable, and conscious control over action and tool use has been gained.

Figure 3 summarizes the structures of the action and emotion systems of humans. Systems that already exist in non-human primates are illustrated in the lower portion of Figure 3 (which is simply a re-depiction of the left portion of Figure 2). They are the action and emotion systems, and are activated through respective mirror neuron systems. Both share three output channels: somatic (including facial), vocal and autonomic effects.

The shaded region located centrally at the top of Figure 3 depicts the systems that developed in humans (see Box 1). That is, the subjective self emerged through tool use in resonance with the theory of mind system. This system, through newly developed TPJ–IPS connections, became able to communicate with action systems and produce conscious bodily actions (thick red arrow). The body somatic system sends motor signals to the limbs and torso through the spinal cord, whereas the facial somatic system controls facial expressions through the brainstem. This facial somatic system was originally purely emotional, but humans acquired enough voluntary control of it to reproduce pseudo-emotional expressions, such as a forced smile. Because intracortical connections are almost always reciprocal, the IPS mirror system should feed information about the form of an action back to the TPJ, the subjective-self system. Thus, the form of action can be recognized independently of its drive and context. This internal (intrabrain) loop circuit makes true imitation possible in humans.

The emotion system produces autonomic output. Even in humans, this system is not fully controlled by subjective self, because there is no direct feedback from the emotional system to the cognitive self. Yet, one might recognize emotional state through indirect feedback from emotional autonomic reactions, and this could be an emotional somatic marker (see glossary) [39].

Voluntary control of the vocal system is fully developed in humans to enable spoken language. In animals, vocalizations are usually tightly linked with their emotional states. We have recently discovered, however, that when tool-use training was combined with vocal production learning, monkeys could develop volitional reference calls (see glossary) — which is unheard of in wild monkeys [40].

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**Figure 3**

The human action production system has three major components: emotion, action and self and/or cognition (written in thick black text). The outlining gray text represents neural substrates that trigger these major components, through gray arrows, to operate. The green shaded area at the top in the middle indicates systems unique to humans. Thick green arrows indicate the output of action, and emotion through action, system (see text). The thick red arrows indicate conscious control of actions by the subjective self, which is unique to humans, but can be induced to a lesser degree in monkeys through tool-use training. The thick blue arrow indicates feedback about form of actions, resulting in “true imitation” mechanisms. Dashed pink and blue lines indicate incomplete emotional self-control circuitry.
Judging from the changes in latency and other observations during the several days-long training process, these calls initially required extreme effort. It was as if the emotional call pathways (see glossary) were being recruited at first through intracortical connections — although this remains hypothetical — followed by gradual transfer to direct pathways and finally to voluntary vocal actions. Similar to somatic actions, as described above, imitation circuitry should also be in place for vocal actions. Similar to somatic actions, as described above, as an external object. This would lead to two important aspects emerging in the mind of the tool-user: first, explicitly realizing that one’s own body is composed of multiple parts that are spatially arranged and intentionally controllable; and second, that those body parts could be compatible (both functionally and structurally) with external objects, namely tools. This establishment of parity between body parts and tools enables tool users to incorporate (or assimilate) tools into their own body schemas. Moreover, tool users can then ‘objectify’ their own body parts, and eventually should be able to objectify themselves entirely — to observe themselves mentally from a third-person perspective. This progression should contribute greatly to the development of true imitation, by which the form of an action can be extracted (through the mirror neuron system) and treated independently of its goal, as a consciously recognized, independent object. Finally, we might hypothesize that these ‘self-objectification’ processes establish equivalence in the mind of the agent between other agents and the self, including understanding that tools are equally compatible for both. The result is a human social structure in which mutual evaluation of graceful, refined actions really matters.

**Conclusions**

An important problem for the tool-using brain to solve is how to ‘regard’ a tool — as one’s own body-part or merely

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**Box 1 Human-specific neural substrates**

Could there be a human-specific neural substrate constituting the large-scale intracortical networks described here? On the basis of fragmentary evidence in the literature, I postulate potential mechanisms that could fit the bill.

The magnopyramidal neurons (see glossary) reported by Braak [41], as well as acetycholinesterase-rich magnopyramidal neurons described later in relation [42–44], could be the candidates. These neurons reside only in layer III of the human cerebral cortex, particularly in the cortices related to higher cognitive functions such as language. These cortices include the ventral premotor area including Broca’s area; the intraparietal area including the supramarginal gyrus; the superior temporal area including Wernicke’s area; and the medial prefrontal cortex and part of visual cortex [41–44], all of which are members of the network proposed here. Given that large pyramidal neurons have long-range axonal projections, it is plausible that these neurons contribute to these networks. Another candidate is the Von Economo spindle neurons [45,46], which are located in anterior medial prefrontal cortex. These cells also have long-range intracortical connections, and when deficient are hypothesized to retard retardation and lead to autistic disorders [46].

Common features between the mirror neuron systems in normal subjects and the deficits seen in autistic spectrum disorders (see glossary) have fuelled speculation that these disorders arise from mirror neuron system dysfunction [47,48]. Dysfunction of the amygdala (that is associated with emotional processing and involved in the affective mirror neuron system) and TPJ (that is associated with theory of mind function) could also be involved in autistic disorders [49]. This circuitry is impaired in alexithymic patients, who lack the ability to understand and interpret not only other’s emotions, but also their own [50].

Macaque monkeys have a mirror neuron system, yet they neither imitate nor show evidence of a theory of mind. Thus, for the human mirror neuron system to enable both true imitation and theory of mind, some new functions must have been added to it. The fact that non-human primates can be trained in the laboratory to exhibit human-like behaviors that never manifest in the wild suggests that monkeys possess latent or dormant precursors for human-level mental abilities. Children that are severely retarded in social interactions can similarly be trained to exhibit imitation behavior using applied behavioral analysis procedures [51]. This might be possible in these children through the recruitment of similarly hidden network circuitry, and thus could shed light on how training non-human primates brings forth more human-like behaviors. And finally, I would like to suggest that tool-use tasks would be even more effective at inducing such improvements.

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**References and recommended reading**

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest


This theoretical article tries to bridge the gap between the known properties of the monkey and the human mirror neuron systems, in which the monkey system has only action understanding, whereas the human system also has imitation and language functions. Conceptual and computational approaches are compared to highlight the research efforts required from both sides to reduce the gap.
This review summarizes the currently emerging field of emotional body cognition. It highlights how mirror neurons in the ventral premotor cortex of rhesus monkeys attribute about others’ tool using skills. It articulates body motions and consequent static posture: a means-ends tool choice in cotton-top tamarins. Emotional communication in Japanese macaques involves joint attention. Reflections of other minds: how means-end tool use in cotton-top tamarins. The specialized structure of human language cortex: pyramidal cell size asymmetries within auditory and language cortices: regional variation of AChE-rich magnopyramidal neurons have a left-right size asymmetry in Broca’s area. A neuronal morphologic type unique to humans and great apes save tools for future use. Cebus apella: symmetrical brain asymmetries and interactions. The somatic marker hypothesis and the possible functions of the prefrontal cortex. The authors use evoked potential mapping and transcranial magnetic induction of novel connections in the adult monkey cerebral cortex that are induced by demanding behavioral learning. The authors of this neuroanatomical study describe how two weeks of tool-use training forges a novel cortico–cortical connection linking the intraparietal area and temporoparietal junction. This newly forged link is formed by slight extension of already existing axonal projections on to the vicinity of the former area. The results provide the first evidence for induction of novel connections in the adult monkey cerebral cortex that are induced by demanding behavioral learning.


The authors use evoked potential mapping and transcranial magnetic stimulation together with epileptic seizure focus analysis to show that the temporoparietal junction is the crucial area for conscious experience of the self through spatial unity of the mind and the body.


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