Tools for the body (schema)

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What happens in our brain when we use a tool to reach for a distant object? Recent neurophysiological, psychological and neuropsychological research suggests that this extended motor capability is followed by changes in specific neural networks that hold an updated map of body shape and posture (the putative 'Body Schema' of classical neurology). These changes are compatible with the notion of the inclusion of tools in the 'Body Schema', as if our own effector (e.g. the hand) were elongated to the tip of the tool. In this review we present empirical support for this intriguing idea from both single-neuron recordings in the monkey brain and behavioural performance of normal and brain-damaged humans. These relatively simple neural and behavioural aspects of tool-use shed light on more complex evolutionary and cognitive aspects of body representation and multisensory space coding for action.

To act efficiently in space, our brain must not only localize any objects of interest in extrapersonal space but also hold a constantly updated status of the body shape and posture. The 'Body Schema' of classical neurology [1,2] originally indicated this status as an ongoing, mainly unconscious integration of successive proprioceptive signals [1], sometimes in contrast to a more conscious knowledge about the body – the 'Body Image' [3]. The somewhat anecdotal concept of body schema has been greatly enriched by modern neuroscience [4,5].

First it has been found that besides proprioception, other sensory modalities (typically somatosensory and visual) are crucial to its construction [5–12]. Second, single-neuron recordings in the monkey brain have changed the vision of a 'purely perceptual' construction of a body map in the brain towards a more multi-componental, action-oriented one. In this view, multiple fronto-parietal networks integrate information from discrete regions of the body surface and external space in a way which is functionally relevant to specific actions performed by different body parts (e.g. [13–17]).

Of particular interest to this review is the discovery of premotor, parietal and putaminal neurons that respond both to somatosensory information from a given body region (i.e. the somatosensory Receptive Field; sRF), and to visual information from the space (visual Receptive Field; vRF) adjacent to it [18–20]. Importantly, for some such bimodal neurons, the vRF remains anchored to the body part when this is moved in space [16,18]. This system may be crucial for coding action space in coordinates centred on the body [13,15,16,21]. In this review we will refer to the widely [4,5,22–25] but perhaps ambiguously [26] used term Body Schema, or to 'body representation' to indicate such a neural system whereby space coding for action is centred on constantly updated, multisensory information about the body.

Tool-use: a clue to the plasticity of body representation and space coding

Although the length of our effectors (mainly the arms) limits our action space, we can use many different tools (from forks to pick up hot food to hyper-technological telesurgery devices) to extend our physical body structure and, consequently, our action space.

Early intuitions (e.g. [1]) suggested that manipulated objects, or items of clothing [27,28] become 'incorporated into the body schema'. In recent years there has been an explosion of interest in trying to verify such an intriguing hypothesis.

The simple model used in many experiments discussed in the present review is to observe changes in the behaviour and/or the neural activity of monkeys and humans following the use of simple tools (for example a rake) to extend reaching space. Such data are important both for gaining further knowledge about the plasticity of body representations in the brain, and to develop new technological tools. Furthermore they allow speculation about the possibilities of 'intelligent' use of simple and complex tools in monkeys.

Neurophysiology of tool-use in macaque monkeys

Japanese macaques can be trained to be dexterous tool-users [29], even though they rarely exhibit tool-use behaviour in their natural habitat (see Box 1). After two weeks of training [30], when a food pellet was dispensed beyond the reach of the hands, monkeys skilfully used a rake to pull the food closer, where they could reach it with their unaided hand. Thus, the tool effectively extended the animals' reaching distance. In these monkeys, neuronal activity was recorded from the intraparietal cortex, where somatosensory and visual information is integrated. Neurons responding to both somatosensory and visual stimulation, namely 'bimodal neurons', were analysed (Figure 1).

Some of these neurons responded to somatosensory stimuli at the hand (Figure 1a), and to visual stimuli near the hand (Figure 1b). Furthermore, their vRF followed the hand when this was moved in space. Crucially, in some of these bimodal neurons the vRFs expanded to include the entire length of the tool, after the monkey had performed

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Box 1. Genetic recruitment of evolutionary precursors?

Before Köhler's classical findings in chimpanzees [59], tool-use was believed to be peculiar to humans. It is still the case that evidence for consistent tool-use is rather fragmented in lower primates and even in great apes other than chimpanzees [60]. Old world macaque monkeys seldom use tools. In particular, the existence of spontaneous use is uncertain, whereas this is more frequent in New world monkeys [60]. Such sporadic emergence of tool-use in different primates led us to think about the mental and neural substrates that are essential for tool-using behaviours. A key question is whether there are differences in the neural machinery among different primates corresponding to their tool-use abilities, or whether they could show the ability to use tools whenever particular conditions are met.

Although Japanese macaques rarely use tools spontaneously in the wild [60] they could be trained to use a rake to retrieve distant food [30] – the evidence for this has so far been confirmed in over thirty individuals. The training took about two weeks (never less than this) to accomplish. During the learning phase, augmented expression of immediate-early-genes [50], neurotrophic factors (BDNF, NT-3) and receptor *trk*B [51,52] were observed. This expression might represent a genetic indicator of

tool-use learning, as it was found selectively in the intraparietal area, which has been shown to contain bimodal neurons with expanding visual receptive fields with tool-use (see main text), and was no longer found once the learning was complete. The above training-dependent genetic expression might induce a reorganization of the neural circuitry with the appearance of novel bimodal somatosensory-visual response properties in some neurons [61,62]. This, in turn, might be the substrate for coding a modified body representation following tool-use.

Given the above evidence, we could imagine that some precursor (or basic building block) of human tool-use ability was already furnished in the brain of our common ancestor with monkeys, and was pushed to full expression by some sort of 'evolutionary pressure'. Demanding training might mimic such a pressure and activate some silent neurogenetic mechanisms. Similar genetic mechanisms could be present for some other functions, not spontaneously expressed in the wild. Exploring this issue would not only shed light on developmental and evolutionary aspects of higher cognitive functions in primates, but might provide an intriguing viewpoint on the potential, unexpressed faculties of the intact and brain-damaged human brain.

five minutes of food retrieval with the handheld rake (Figure 1c). Bimodal neurons with the above properties were named 'distal type' neurons. Other bimodal neurons with sRFs located around shoulder/neck (named 'proximal type', Figure 1e) had vRFs covering the space reached by the arm (Figure 1f). After tool-use, these proximal vRFs

expanded to code the space now accessible with the rake (Figure 1g).

Such vRF expansions may constitute the neural substrate of use-dependent assimilation of the tool into the body schema, suggested by classical neurology [1] (see also Box 2). Hence, any expansion of the vRF only followed
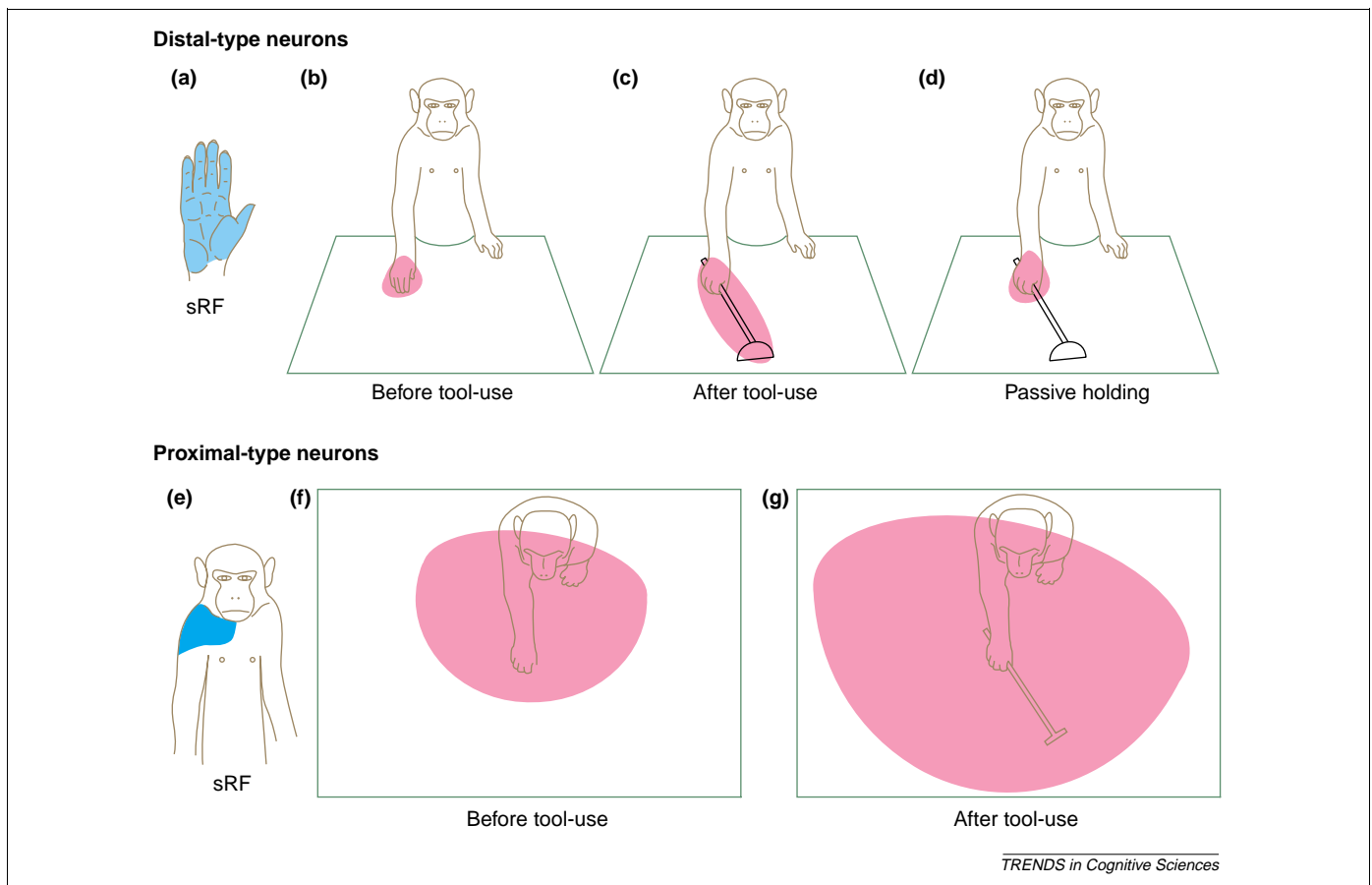
Figure 1. Changes in bimodal receptive field properties following tool-use. The somatosensory receptive fields (sRF) of cells in this region were identified by light touches, passive manipulation of joints or active hand-use. The visual RF (vRF) was defined as the area in which cellular responses were evoked by visual probes (the most effective ones being those moving towards the sRF). **(a)** sRF (blue area) of the 'distal type' bimodal neurons and their vRF (pink areas) **(b)** before tool-use, **(c)** immediately after tool-use, and **(d)** when just passively grabbing the rake. **(e)** sRF (blue area) of 'proximal type' bimodal neurons, and their vRF (pink areas) **(f)** before and **(g)** immediately after tool-use.

Box 2. Looking for neural correlates of acting in virtual reality environments

When playing video games, or using tele-operator systems, we feel that our self-image is projected into the video monitor as a functional extension of the body. A general previously held belief was that monkeys, and even great apes, were able to use visual images on a video monitor to guide bodily movements but could not recognize their body parts observed in the monitor as their own [60,63]. The above conclusion was drawn through simple behavioural analyses without any empirical measure of monkeys' 'introspection', which was considered to be impossible to obtain.

However, in one of our studies we trained monkeys to use tools under visual feedback provided through video-captured images projected on a monitor [64] (Figure Ia). After training, visual receptive fields (vRFs) of intraparietal bimodal neurons (with a somatosensory RF on the hand; Figure Ic) were formed around the image of the monkey's hand in the monitor (Figure Id). This was assessed using an artificial visual probe superimposed on the visual image of the hand by a video signal generator (called a 'Chromakeyer', Figure Ib). After tool-use, the vRF around the image of the hand on the monitor extended along the image of the handheld rake (Figure Ie), like the vRF extension when viewing the hand directly (see Figure 1 in main text). In other conditions in

the experiment, the size and position of the vRFs of these bimodal neurons were modified in line with expansion (Figure Ig), compression (Figure Ih), or displacement (Figure Ii) of the hand's image in the video monitor, even though the posture and position (and of course size!) of the real hand remained constant. Furthermore, vRFs for the same neurons were formed around a restricted spot left around the tip of the tool (akin to a computer cursor) when all other images on the monitor were filtered out (Figure If).

These results suggest that the visual image of the hand (and even its 'virtual' equivalent, such as a spot of light) in the monitor is treated by the monkeys as an extension of their own body. Moreover the causal/action space around the hand's image in the monitor might be also extended, as suggested by the sudden retraction of the animal's own hand when the image of a snake or spider approached the image of the hand in the monitor [64].

These intraparietal cortical neurons might therefore constitute a possible neural substrate of the human observer's feeling of a sense of 'reality' or 'presence' [65] when dealing with a virtual apparatus or a video game.
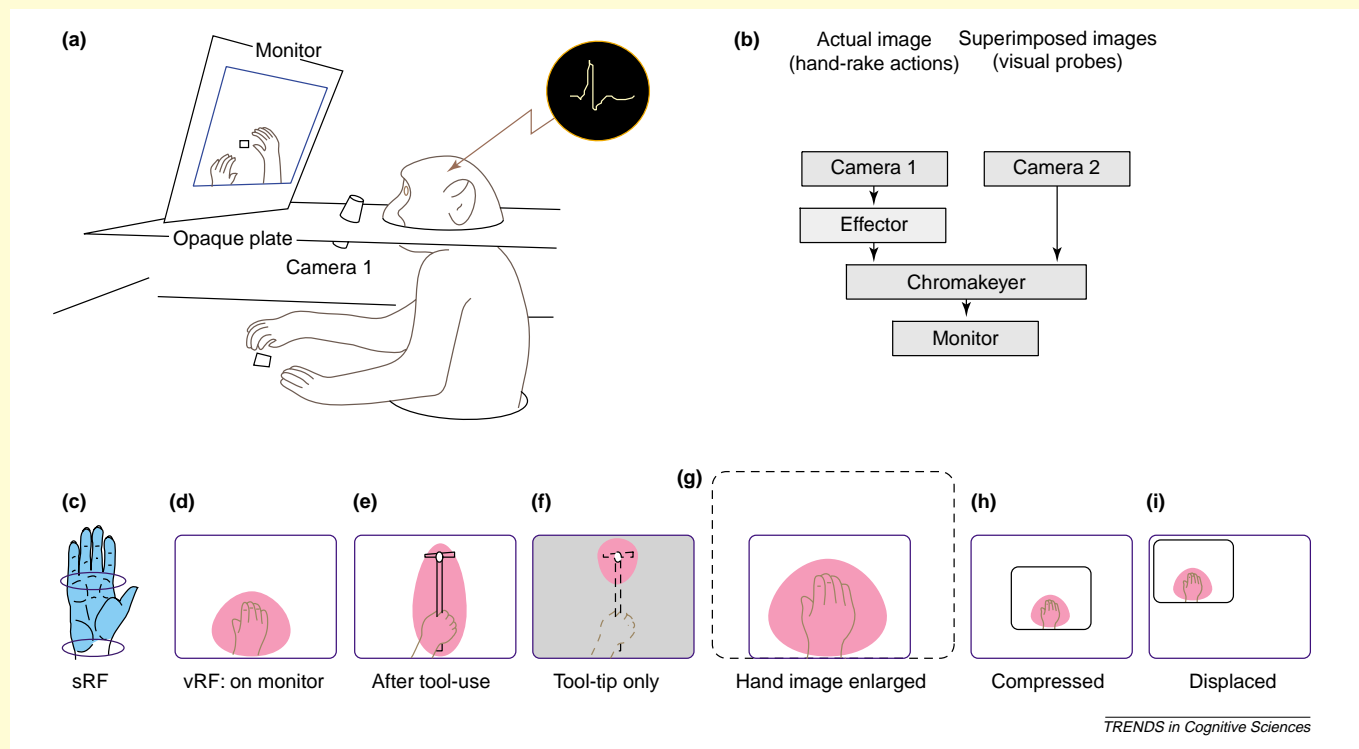
Figure I. Neural correlates of tool-use under indirect visual control. **(a)** Neural responses are recorded (inset) while monkeys retrieve items of food and observe their actions on a video monitor, as captured by a video camera (Camera 1). **(b)** The visual scene observed by the animal can be modified by adding superimposed images (via a special device called 'Chromakeyer') on a neutral background, recorded by a second video camera (Camera 2), or by altering the position and size of visual images using special filters ('Effector'). **(c)** The somatosensory receptive field (sRF) and **(d–i)** visual receptive field (vRF) in different viewing conditions (see text for details). Adapted from [64].

active, intentional usage of the tool, not its mere grasping by the hand (Figure 1d).

Furthermore, the vRF expansion was found in parietal neurons with sRFs on the arm/hand, but not in those with sRFs on the fingers. This might reflect the fact that a rake represents a functional extension of the hand and forearm, but not of the fingers, because it allows only reaching but not a precision-grip. This assumption would raise the intriguing question of whether bimodal neurons coding for the finger area would show expansion of their vRF

after training with tools allowing a precision-grip (such as pliers).

Behavioural effects of tool-use in normal humans

Inspired by the experiments on macaque monkeys described above, several researchers have recently investigated the behavioural effects of tool-use in human observers, in order to ascertain whether similar neural mechanisms exist in the two species. These studies share a basic logic; that is, to identify whether tool-assisted

reaching for stimuli presented beyond the hand's normal or unaided reach would produce similar behavioural effects as direct reaching for nearby stimuli (i.e. in reachable space) with the hands alone. If this were confirmed, it would suggest that the tool became incorporated into a putative brain representation of the hand wielding it [1] and that visual stimuli presented at the tip of the tool might be coded by the brain in a similar fashion to those presented directly at the hand [29].

Crossing hands and crossing tools

It has been found that, when wielding tools in a crossed posture, behavioural effects reverse in a similar way to when the hands themselves are crossed. For example, temporal order judgements of vibrations are disrupted to a similar degree both when stimuli are delivered to crossed, as opposed to uncrossed hands, and when stimuli are delivered to the far tips of crossed, as opposed to uncrossed, hand-held sticks [31]. Thus, somatosensory stimuli are similarly localized when delivered either to the skin directly, or indirectly via long tools (cf. [32] for related results in a spatial compatibility task), as if the tip of the tool becomes a functional extension of the body into far space.

Further studies addressed the question of whether behavioural effects of crossed tools extend to crossmodal effects, to search for similarities with monkey data (as well as avoiding any possible stimulus–response compatibility implications of previous studies). Maravita and colleagues [33] used a crossmodal (somatosensory–visual) interference task widely used to study crossmodal attention (see [34,35] for details). Briefly, in this task, small LED flashes (visual distractors) at the fingertips typically produce interference in localizing simultaneously activated vibrotactile targets. Importantly, interference is stronger for the hand located on the same side (ipsilateral) as the visual distractors than for the hand on the opposite side (contralateral). However, when the hands are crossed to contact contralateral distractors, the effect reverses: visual distractors interfere more with localization of somatosensory targets delivered to the anatomically *contralateral* hand (which is now ipsilateral in external space) which they now touch. In their experiment Maravita and colleagues found that, with tools held by the tactually stimulated hands and visual distractors at the tool tip (Figure 2a), a similar reversal of crossmodal interference (Figure 2c) occurred when each tool-tip contacted visual distractors that were contralateral in external space to the tactually stimulated hand (Figure 2b), although the hand posture remained unchanged. In other words, reaching for a visual stimulus with the hand or with the tip of the tool seems to produce similar crossmodal interference effects. Crucially, such a reversal of visual interference dependent on the tool posture gradually increased with extensive tool-use [33].

Intriguingly, the above effects of tool-use on crossmodal interference are reminiscent of the modified visual responses of bimodal parietal neurons following extensive tool-use in monkeys, and suggest that their occurrence might be mediated by similar multimodal structures. This assumption is supported by recent PET data showing that the use of tongs to grasp and move objects, as compared with direct hand manipulation, activates regions in the intraparietal sulcus [36], corresponding anatomically to the site of electrophysiological recordings in monkeys [29] (although the correspondence of the intraparietal sulcus between the monkey and human brain is, so far, only putative).

Neuropsychological effects of tool-use in brain-damaged patients

Further clues to the behavioural, and possibly neural, implications of tool-use have recently come from brain-damaged patients, particularly those patients who exhibit unilateral spatial neglect or extinction. Neglect patients typically ignore stimuli contralateral to the side of their brain damage (contralesional stimuli) [37], whereas extinction patients can detect unilateral stimuli on both sides of space, but ignore contralesional stimuli only when presented together with competing ipsilesional ones [38]. As we will now discuss, the severity of such syndromes can be modulated by tool-use.

Effects of tool-use on neglect

Berti and Frassinetti [39] examined the effect of tool-use in a brain-damaged patient, P.P., whose neglect selectively affected the space close to her body (near space). When requested to show the mid point of a drawn line, P.P. put her mark further towards the right from the objective midpoint, as typically observed in neglect. However, when lines were presented out of hand's reach (far space), P.P.'s bisections using a laser pointer were flawless. By contrast, when a long stick was used for the same far-line bisection, P.P. showed a rightward bias again. The authors concluded that when the stick made far space reachable, this became automatically coded by a neural network selective for near space (cf. [40]) whereby neglect was selectively present in P.P. (see also [41]). In another similar single-case study [42] bisection errors increased when reaching to lines with a stick, as compared with pointing with a laser pointer, *both* in near and far space. Therefore, in this patient, the crucial factor in determining the amount of neglect was the possibility of performing bisections through *reaching* via the tool, as opposed to pointing, regardless of the space sector in which bisection was performed as in patient P.P. [39].

Effects of tool-use on crossmodal extinction

Altohugh the above studies on neglect suggest that the spatial coding of extrapersonal objects can be effectively influenced by reaching them with a tool, subsequent studies on extinction patients provide further clues to the crossmodal implications of tool-use in humans.

Patients affected by crossmodal extinction show unawareness of contralesional stimuli in one modality (typically a left touch) when a competing ipsilesional stimulus in another modality (typically a right visual stimulus) is presented simultaneously [43,44], even if they are able to detect left or right stimuli when presented in isolation. Crucially, in some such patients stronger tactile extinction on the contralesional (left) hand is induced when visual stimuli are delivered close to the ipsilesional
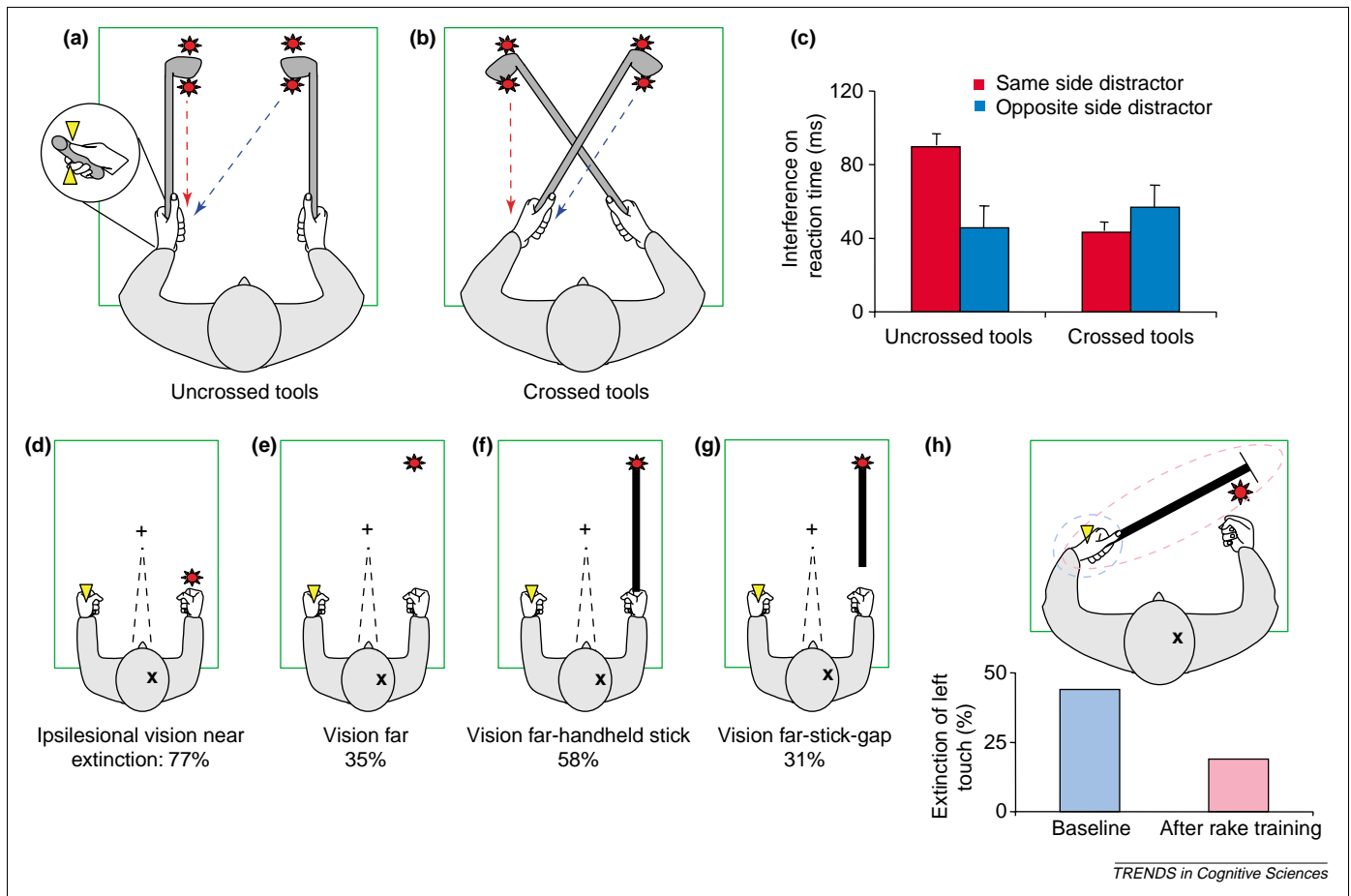
Figure 2. Crossmodal effects of tool-use in humans. **(a–c)** Normal observers were required to judge which of two computerised vibrotactile targets (denoted by yellow triangles throughout) placed under the thumb and finger of either hand was stimulated while wielding two toy-golf clubs. Subjects must respond as quickly as possible and also ignore simultaneous visual distractors (red star symbols throughout), arranged in a similar up/down orientation at the tools' tip. As in other experiments with the stimulated hands in direct contact with visual distractors [35], with uncrossed tools **(a)** the typical somatosensory–visual interference (a slower response for incongruent relative elevation of stimuli and distractors) was stronger from distractors on the same side of space as the stimulated hand (indicated by red arrows; red bars in **(c)**), than from those on the opposite-side (blue arrows, bars). The pattern of interference reverses with crossed tool-tips **(b)**. (Adapted from [33].) **(d–h)** Crossmodal extinction (percentages below each panel) of left touches in patient B.V., who has right-hemisphere damage (denoted by X) Extinction decreased when simultaneous flashes near the right hand **(d)** were moved further away **(e)**. Extinction increased again if the far flash was reached by a long stick **(f)** but not if the stick was disconnected from the hand **(g)**. (Adapted from [45].) **(h)** After ten minutes of rake-assisted reaching with the left hand, left tactile extinction from right flashes at the tool tip decreased (pink bar) compared with the pre-training baseline level (blue bar). The pink dotted oval represents the expansion of a putative hand-centred somatosensory–visual space representation (blue circle) up to the tool-tip following tool-use. This expansion might underlie the reduced competitive extinction. (Adapted from [47].)

(right) hand, than further away from it (Figure 2d,e). This suggests competition at the level of bimodal neurons coding for peri-personal space [21,44].

The above distance-dependent reduction of crossmodal extinction was also observed by Maravita and co-workers (cf. Figure 2d versus 2e) in their right-hemisphere damaged patient B.V. [45]. However, the effect of distance was attenuated (i.e. extinction increased) when B.V. wielded a stick with his ipsilesional hand to touch the position of the far ipsilesional stimulus (Figure 2f), as if the visual stimulus was now closer to the hand (or else the hand itself was moved closer to the stimulus). Crucially, this effect was not seen if the stick was placed upon the table at some distance from the ipsilesional hand (Figure 2g), suggesting that only physically reaching towards the far ipsilesional visual stimulus with the stick increased crossmodal extinction.

The importance of training for these effects of tool-use on extinction was addressed by Farnè and colleagues [46]. In their patients an analogous effect of tool-use to that

found by Maravita and co-workers [45] on crossmodal extinction was obtained only after patients underwent some 'training' with tool-use. Also, in analogy with the experiments in monkeys [29], after a period of rest with the tool passively held on the table, the extinction rate dropped back to the pre-training level.

A similar effect of practice, but with opposite results for extinction, was shown by Maravita and colleagues [47]. Their patient was instructed to reach for the position of an ipsilesional visual stimulus with a rake held by his contralesional hand (Figure 2h, upper panel). In contrast with the results described above, now the link between the left hand and the right space via the tool effectively *reduced* crossmodal extinction between right flashes and left touches (Figure 2h, lower panel). A likely explanation would be that, after training, the two stimuli now fell within a common, bimodal representation of space (Figure 2h, upper panel, pink dotted oval) which expanded from the original hand-centred one (blue dotted circle). In this way, competitive extinction [38] between stimuli on opposite sides of space decreased. Interestingly the

decrease of extinction was only temporary (cf. [29,46]), and its duration was proportional to the duration of the preliminary training.

Intriguingly, whilst in some studies on humans the reported behavioural effects of tool-use occurred without any specific training (e.g. [39,42,45]), in other studies substantial tool-use training was required to elicit these effects [33,46,47]. It might be that simple acts, like pointing [45] or reaching [39,42] with a stick will show behavioural effects without training, whereas more complex tasks involving dextrous use of a tool, such as retrieving objects with a rake [46,47], require some training before any behavioural effects will emerge.

Conclusions

Tool-use represents a huge achievement in human evolution and a distinct way for humans [48] to fulfil many everyday activities. This review has examined a specific aspect of research on tool-use, namely, to what extent the effective use of a tool can induce a plastic

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Box 3. Precursor of mechanistic technology?

Early studies on primate tool-use did not merely witness its occurrence, but also examined to what extent primates could understand the function of given tools or the causal relationship between the intended tool-use and the obtained results. These studies concluded that, although neural mechanisms for object manipulation with tools might be similar in humans and lower primates, huge differences exists in the human and the non-human repertoires and understanding of tool-use: only humans show an insight into causality-based interactions among objects (including tools) in the external world [48,60,66]. It has been suggested that this ability to perceive causal relationships could be crucial to the foundation of modern technology [67].

To explore this issue further, we carried out an experiment in which monkeys were required to use two different tools in combination to retrieve rewards (Figure I, upper row) [68]. The food reward was placed at a distance and was only reachable by a long rake. However, the monkeys could not reach this long rake directly but only by using a second, shorter rake that was within reach but too short to reach the food (Figure Ia). In this situation, monkeys easily solved the problem by using the short rake to pull the long rake's handle closer (Figure Ib–c), grasping the long rake (Figure Id) and finally reaching for the food (Figure Ie). This behaviour was attained very quickly, in remarkable

contrast with the initial basic training in using tools, which took at least two weeks (see Box 1). Thus, once the basic skill in tool-use had been learned through extensive training, the application of such a skill to solve a more complex task could be accomplished rather easily. The possible difference in the neural substrate of such different skills (basic learning versus complex problem solving) was investigated by PET imaging during the execution of a complex task, as depicted in Figure I (lower panels) [69]. Food pellets were delivered into a section of transparent tubing. Monkeys had first to push a food pellet using one rake to make it roll out of the tubing (Figure If); they could then retrieve the food by using a second rake (Figure Ig). By subtracting activations related to single-tool-use from those elicited by the sequential task, prefrontal as well as intraparietal activation was detected (Figure Ih) (cf. [54]).

Further study of such a prefrontal–intraparietal interaction in tasks requiring the understanding of causal relationships between multiple tools under direct vision, or even in 'virtual' conditions [70], could provide clues into the understanding of the causal structure of events in monkeys. Moreover, this would allow speculations on the neural substrates of skilful tool-use in animals (maybe even in non-primates [71–73]) and on the evolutionary precursors of modern technology.

Sequential tool-use
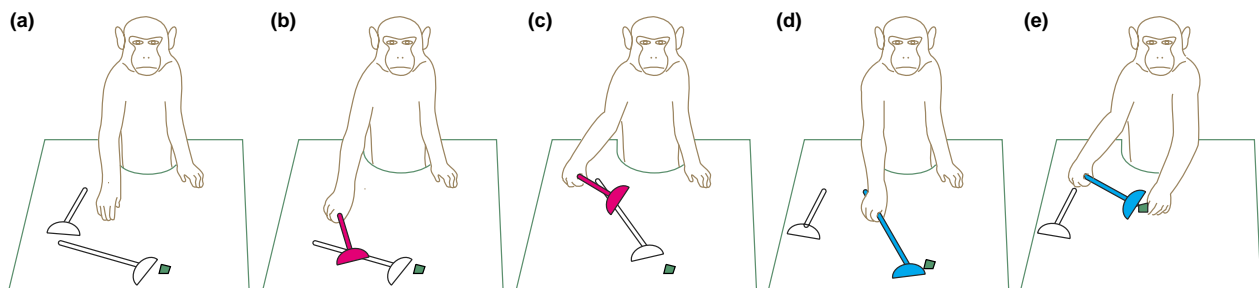
Applied combination
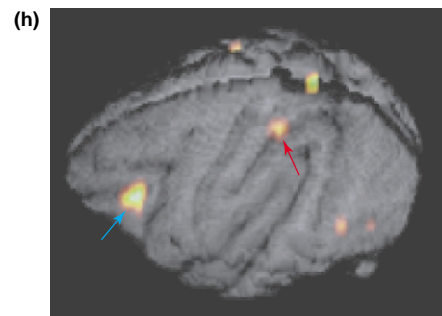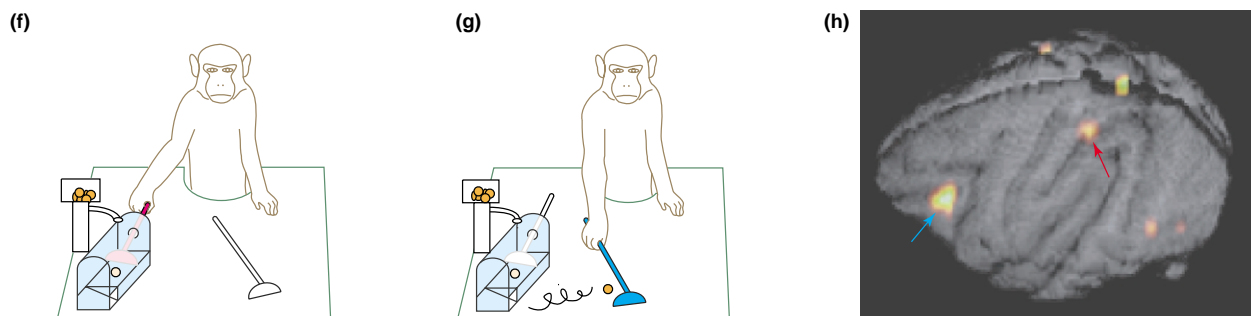
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Figure I. Complex tool-use in monkeys. **(a-e)** Experimental setting for the double-rake reaching study in monkeys. See text for details. (Adapted from [68].) **(f-g)** Experimental setting for a sequential tool-use task, and **(h)** PET imaging brain activation (important intraparietal and prefrontal activation foci showed by red and blue arrow respectively) for the complex tool-use experiment in monkeys. (Adapted from [69]).

modification of the body representation in the brain. This sheds light not only on some basic neural mechanisms of tool-use, but also on some general mechanisms of body representation [4,5] and their relationship with the multimodal representation of extrapersonal space for action (cf. [13,15,16]).

Data presented in this review support the idea that tools, by enabling us to extend our reaching space, can become incorporated into a plastic neural representation of our body [1]. As a consequence, tools might effectively increase the integration of biologically relevant (e.g. [49]) distant visual stimuli in a multimodal, body-centred representation of space. The neural substrate subserving this process of 'internalisation' appears to show some similarities in macaques and humans [5]. However, humans might have such neural machinery present in the brain from birth or early in life, whereas lower primates seem to need a period of training to induce behavioural learning [30], and electrophysiological [29] and even neurogenetic changes in the animal's parietal cortex [50–52].

This review has focussed primarily on some basic neurobiological consequences of the use of simple tools. However it is likely that any tool-dependent changes in the response of multimodal neurons, or even any inclusion of the tool into the body schema, either co-occur or follow other neurobehavioural modifications due to motor learning, especially when using complex tools requiring the previous acquisition of complex motor skills (cf. [53]). In line with this view, a recent PET imaging study in monkeys shows that the use of an effective (versus ineffective) tool is characterized by an intraparietal activation (compatible with single-neuron recordings [29]) accompanied by acticity in a network of premotor, cerebellar and subcortical motor areas [54].

Finally, the possibility of training monkeys to use a *simple* tool does not imply that any degree of human-like, intelligent tool-use can be obtained in monkeys by training. Indeed, the intelligent use of complex tools seems peculiar to the human species, probably as a result of our brain organization and the specialization for praxic skills and linguistic competences (see, for example, [55] in this issue; [48,56–58]). Nonetheless, the study of simple tool-use abilities in lower primates provides fascinating data on how precursors of intellectual abilities (see Boxes 2 and 3) may have co-evolved with tool-use and technology (see Box 4).

References

1 Head, H. and Holmes, G. (1911) Sensory disturbances from cerebral lesions. *Brain* 34, 102–254

2 Bonnier, P. (1905) L'aschématie. *Rev. Neurol.* 13, 605–609

3 Gallagher, S. (1998) Body schema and intentionality. In *The Body and The Self* (Bermudez, J.L. *et al.*, eds), pp. 225–244, MIT Press

4 Berlucchi, G. and Aglioti, S. (1997) The body in the brain: neural bases of corporeal awareness. *Trends Neurosci.* 20, 560–564

5 Maravita, A. *et al.* (2003) Multisensory integration and the body schema: close to hand and within reach. *Curr. Biol.* 13, R531–R539

6 Pavani, F. *et al.* (2000) Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychol. Sci.* 11, 353–359

7 Farnè, A. *et al.* (2000) Left tactile extinction following visual stimulation of a rubber hand. *Brain* 123, 2350–2360

8 Graziano, M.S.A. and Botvinick, M.M. (2002) How the brain represents the body: insights neurophysiology and psychology. In *Common Mechanisms in Perception and Action: Attention and Performance XIX* (Prinz, W. and Hommel, B., eds), pp. 136–157, Oxford University Press

9 Botvinick, M. and Cohen, J. (1998) Rubber hands 'feel' touch that eyes see. *Nature* 391, 756

10 Armel, K.C. and Ramachandran, V.S. (2003) Projecting sensations to external objects: evidence from skin conductance response. *Proc. R. Soc. Lond. B. Biol. Sci.* 270, 1499–1506

11 Maravita, A. *et al.* (2002) Seeing your own touched hands in a mirror modulates cross-modal interactions. *Psychol. Sci.* 13, 350–355

12 Schilder, P. (1935) *The Image and Appearance of the Human Body: Studies in the Constructive Energies of the Psyche*, Kegan Paul

13 Colby, C.L. (1998) Action-oriented spatial reference frames in cortex. *Neuron* 20, 15–24

14 Rizzolatti, G. *et al.* (1998) The organization of the cortical motor system: new concepts. *Electroencephalogr. Clin. Neurophysiol.* 106, 283–296

15 Rizzolatti, G. *et al.* (1997) The space around us. *Science* 277, 190–191

16 Graziano, M.S. and Gross, C.G. (1998) Spatial maps for the control of movement. *Curr. Opin. Neurobiol.* 8, 195–201

17 Jeannerod, M. *et al.* (1995) Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci.* 18, 314–320

18 Graziano, M.S. *et al.* (1994) Coding of visual space by premotor neurons. *Science* 266, 1054–1057

19 Fogassi, L. *et al.* (1996) Coding of peripersonal space in inferior premotor cortex (area f4). *J. Neurophysiol.* 76, 141–157

20 Duhamel, J-R. *et al.* (1998) Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *J. Neurophysiol.* 79, 126–136

21 Làdavas, E. (2002) Functional and dynamic properties of visual peripersonal space. *Trends Cogn. Sci.* 6, 17–22

22 Critchley, M. (1953) Disorders of the body-image. In *The Parietal Lobe* (Critchley, M., ed.), pp. 225–255, Hafner Press

23 Coslett, H.B. (1998) Evidence for a disturbance of the body schema in neglect. *Brain Cogn.* 37, 527–544

24 Cumming, W.J. (1988) The neurobiology of the body schema. *Br. J. Psychiatry Suppl.*, 7–11

25 Denes, G. (1990) Disorders of body awareness and body knowledge. In *Handbook of Neuropsychology* (Vol. 2) (Boller, F. and Grafman, J., eds), pp. 207–228, Elsevier

26 Poeck, K. and Orgass, B. (1971) The concept of the body schema: a critical review and some experimental results. *Cortex* 7, 254–277

27 Critchley, M. (1979) *The Divine Banquet of the Brain and Other Essays*, Raven Press

28 Aglioti, S. *et al.* (1996) Disownership of left hand and objects related to it in a patient with right brain damage. *Neuroreport* 8, 293–296

29 Iriki, A. *et al.* (1996) Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7, 2325–2330

30 Ishibashi, H. *et al.* (2000) Acquisition and development of monkey tool-use: behavioural and kinematic analyses. *Can. J. Physiol. Pharmacol.* 78, 1–9

31 Yamamoto, S. and Kitazawa, S. (2001) Sensation at the tips of invisible tools. *Nat. Neurosci.* 4, 979–980

32 Riggio, L. *et al.* (1986) What is crossed in crossed-hand effects? *Acta Psychol. (Amst.)* 62, 89–100

33 Maravita, A. *et al.* (2002) Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition* 83, B25–B34

34 Driver, J. and Spence, C. (1998) Attention and the crossmodal construction of space. *Trends Cogn. Sci.* 2, 254–262

35 Spence, C. *et al.* Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task. *J. Physiol. (Paris)* (in press)

36 Inoue, K. *et al.* (2001) Activation in the ipsilateral posterior parietal cortex during tool use: a pet study. *Neuroimage* 14, 1469–1475

37 Bisiach, E. and Vallar, G. (2000) Unilateral neglect in humans. In *Handbook of Neuropsychology* (Boller, F. and Grafman, J., eds), pp. 459–502, Elsevier

38 Driver, J. *et al.* (1997) Extinction as a paradigm measure of attentional bias and restricted capacity following brain injury. In *Parietal Lobe Contributions to Orientation in 3d Space* (Thier, P. and Karnath, H-O., eds), pp. 401–429, Springer Verlag

39 Berti, A. and Frassinetti, F. (2000) When far becomes near: re-mapping of space by tool use. *J. Cogn. Neurosci.* 12, 415–420

40 Rizzolatti, G. *et al.* (1983) Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. *Brain* 106, 655–673

41 Ackroyd, K. *et al.* (2002) Widening the sphere of influence: using a tool to extend extrapersonal visual space in a patient with severe neglect. *Neurocase* 8, 1–12

42 Pegna, A.J. *et al.* (2001) So near yet so far: neglect in far or near space depends on tool use. *Ann. Neurol.* 50, 820–822

43 Mattingley, J.B. *et al.* (1997) Attentional competition between modalities: extinction between touch and vision after right hemisphere damage. *Neuropsychologia* 35, 867–880

44 di Pellegrino, G. *et al.* (1997) Seeing where your hands are. *Nature* 388, 730

45 Maravita, A. *et al.* (2001) Reaching with a tool extends visual–tactile interactions into far space: evidence from cross-modal extinction. *Neuropsychologia* 39, 580–585

46 Farnè, A. and Làdavas, E. (2000) Dynamic size-change of hand peripersonal space following tool use. *Neuroreport* 11, 1645–1649

47 Maravita, A. *et al.* (2002) Active tool-use with contralesional hand can reduce crossmodal extinction of touch on that hand. *Neurocase* 8, 411–416

48 Johnson-Frey, S.H. (2003) What's so special about human tool use? *Neuron* 39, 201–204

49 Cooke, D.F. *et al.* (2003) Complex movements evoked by microstimulation of the ventral intraparietal area. *Proc. Natl. Acad. Sci. U. S. A.* 100, 6163–6168

50 Ishibashi, H. *et al.* (1999) Immediate-early-gene-expression by the training of tool-use in the monkey intraparietal cortex. *Soc. Neurosci. Abstr.* 25, 889

51 Ishibashi, H. *et al.* (2002) Tool-use learning induces BDNF expression in a selective portion of monkey anterior parietal cortex. *Brain Res. Mol. Brain Res.* 102, 110–112

52 Ishibashi, H. *et al.* (2002) Tool-use learning selectively induces expression of brain-derived neurotrophic factor, its receptor trkB, and neurotrophin 3 in the intraparietal multisensory cortex of monkeys. *Brain Res. Cogn. Brain Res.* 14, 3–9

53 Imamizu, H. *et al.* (2000) Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature* 403, 192–195

54 Obayashi, S. *et al.* (2001) Functional brain mapping of monkey tool use. *Neuroimage* 14, 853–861

55 Johnson-Frey, S.H. (2004) The neural bases of complex tool use in humans. *Trends Cogn. Sci.* 8, 71–78

56 Moll, J. *et al.* (2000) Functional MRI correlates of real and imagined tool-use pantomimes. *Neurology* 54, 1331–1336

57 Goldenberg, G. and Hagmann, S. (1998) Tool use and mechanical problem solving in apraxia. *Neuropsychologia* 36, 581–589

58 Paillard, J. (1993) The hand and the tool: the functional architecture of human technical skills. In *The Use of Tools by Human and Non-Human Primates* (Berthelet, A. and Chavaillon, J., eds), pp. 36–46, Oxford University Press

59 Kohler, W. (1927) *The Mentality of Apes*, Humanities Press

60 Tomasello, M. and Call, J. (1997) *Primate Cognition*, Oxford University Press

61 Hihara, S. *et al.* (2002) Cortical connections of monkey intraparietal cortex representing modified body-images during tool-use. *Soc. Neurosci. Abstr.*, 28219

62 Hihara, S. *et al.* (2003) Sprouting of terminal arborizations of the temporoparietal afferents by tool-use learning in adult monkeys. *Soc. Neurosci. Abstr.*, 93915

63 Matsuzawa, T. ed. (2001) *Primate Origins of Human Cognition and Behaviour* Springer

64 Iriki, A. *et al.* (2001) Self-images in the video monitor coded by monkey intraparietal neurons. *Neurosci. Res.* 40, 163–173

65 Loomis, J. (1992) Distal attribution and presence. *Presence* 1, 113–119

66 Povinelli, D. (2000) *Folk Physics for Apes*, Oxford University Press

67 Wolpert, L. (2003) Causal belief and the origins of technology. *Philos. Trans. R. Soc. Lond. Ser. A Math. Phys. Eng. Sci.* 361, 1709–1719

68 Hihara, S. *et al.* (2003) Rapid learning of sequential tool use by macaque monkeys. *Physiol. Behav.* 78, 427–434

69 Obayashi, S. *et al.* (2002) Macaque prefrontal activity associated with extensive tool use. *Neuroreport* 13, 2349–2354

70 Obayashi, S. *et al.* (2003) Monkey brain areas underlying remote-controlled operations. *Eur. J. Neurosci.* (in press)

71 Hunt, G.R. and Gray, R.D. (2003) Diversification and cumulative evolution in new caledonian crow tool manufacture. *Proc. R. Soc. Lond. B. Biol. Sci.* 270, 867–874

72 Chappell, J. and Kacelnik, A. (2002) Tool selectivity in a non-primate, the new caledonian crow (corvus moneduloides). *Anim. Cogn.* 5, 71–78

73 Anderson, J.R. (2002) Gone fishing: tool use in animals. *Biologist (London)* 49, 15–18

74 Farnè, A. *et al.* (2003) Tool use modifies the multisensory coding of peripersonal space. In *6th IBRO World Congress of Neuroscience*, IBRO, p. 23

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