

Extending or projecting peripersonal space with tools? Multisensory interactions highlight only the distal and proximal ends of tools

Nicholas P. Holmes^{a,*}, Gemma A. Calvert^b, Charles Spence^a

^a Department of Experimental Psychology, South Parks Road, Oxford, OX13UD, Oxford University, UK

^b Department of Psychology, Bath University, Bath, UK

Received 25 June 2004; received in revised form 10 August 2004; accepted 3 September 2004

Abstract

The effects of tool-use on the brain's representation of the body and of the space surrounding the body ('peripersonal space') has recently been studied within a number of disciplines in cognitive neuroscience, and is also of great interest to philosophers and behavioural ecologists. To date, most experimental findings suggest that tool-use extends the boundary of peripersonal space—visual stimuli presented at the tips of tools interact more with simultaneous tactile stimuli presented at the hands than visual stimuli presented at the same distance, but not associated with the tools. We studied the proposed extension of peripersonal space by tool-use by measuring the effects of three different tool-use tasks on the integration of visual and tactile stimuli at three distances from participants' hands along two hand-held tools. When the tool-use task required using the shafts or the tips of the tools, visuotactile interactions were stronger at the tips of the tools than in the middle of the shaft. When the handles of the tools were used, however, visuotactile interactions were strongest near the hands and decreased with distance along the tools. These results suggest that tools do not simply 'extend' peripersonal space, but that just the tips of tools actively manipulated in extrapersonal space are incorporated into the brain's visuotactile representations of the body and of peripersonal space.

© 2004 Elsevier Ireland Ltd. All rights reserved.

Keywords: Tool-use; Peripersonal space; Multisensory; Crossmodal congruency

The proficient use of tools by humans and animals requires the effective integration of multisensory information relating to the body, to the tool(s), and to the space around the body and the tool(s). Recent studies of visuotactile interactions during or following active tool-use behaviours in macaque monkeys [8], neuropsychological patients [2,3], and healthy human participants [19] have often been interpreted as showing that tool-use results in an extension of the neural representation of visuotactile peripersonal space (defined as the space immediately surrounding our bodies [7]). One proposed mechanism for this extension of peripersonal space is the plastic alteration of the size and elongation of the visual receptive fields (VRFs) of multisensory neurons in the posterior parietal and/or the ventral premotor cortex [8,12,17,18] (see Fig. 1A).

If peripersonal space extends along the axis of a tool during tool-use, then the typical properties of visuotactile peripersonal space, as measured, for example, near the hands of the tool-user, should also extend along the tools held in each hand. Two basic properties of visuotactile peripersonal space, as measured with single unit recordings in macaque monkeys [5], are that (a) VRFs are 'anchored' to, or centred on, the corresponding somatosensory receptive fields (SRFs, typically on the hands, arms, face, or head); and (b) that the firing rate of these neurons decreases with the distance of the visual stimulus from the SRF. Thus, if an extension of visuotactile peripersonal space was the only mechanism for mediating the effects of tool-use on visuotactile interactions, as measured either in macaque monkeys, human neuropsychological patients, or in healthy human participants, then the following two predictions arise: (1) Visuotactile interactions should be significantly stronger when both visual and tactile stimuli are applied to the same tool (i.e., within the same hand-centred VRF), than for stimuli applied to different tools; and (2) Vi-

* Corresponding author. Tel.: +44 1865 271 307; fax: +44 1865 310 447.

E-mail address: nicholas.holmes@psy.ox.ac.uk (N.P. Holmes).

URL: <http://www.psy.ox.ac.uk/xmodal/default.htm> (N.P. Holmes).

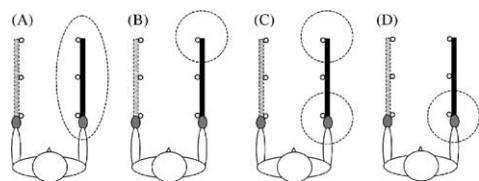


Fig. 1. Four alternative hypotheses regarding the effects of tool-use on the visuotactile representation of peripersonal space. Each figure depicts a human participant holding two tools. The possible experimental outcomes are illustrated for the right hand tool only, though, presumably, both tools should be similarly affected. The small open circles along the tools represent the positions of the visual distractors used in the present experiments. The large broken ellipses represent the putative visual receptive fields (VRFs) of bimodal neurons mediating the effects of tool-use on visuotactile interactions in peripersonal space. (A) Tool-use extends peripersonal space—VRFs expand along the tool shafts and encompass the entire tool. (B) Tool-use leads to a projection of peripersonal space—VRFs around the hands are shifted or projected to the tips of the tools. (C) Tool-use results in new VRFs forming around the tips of the tools—the original receptive fields near the hands remain unchanged. (D) Tool-use has no effect on the VRFs of bimodal neurons. Hypotheses (A–C) are equally compatible with the majority of published human experimental literature on tool-use.

suotactile interactions should be strongest near the hands of the tool-user, and decrease with increasing distance from the hands along the tools.

While several previous studies have demonstrated enhanced visuotactile interactions for visual stimuli presented to the same tool as the simultaneously-applied tactile stimuli (i.e., prediction 1, [12,15–19]), the second prediction of the ‘extending peripersonal space’ hypothesis has not yet been tested empirically in humans. In these previous studies, visual stimuli were typically applied only to the tips of actively used tools, and not near the hands, or in the middle of the shafts of the tools. Furthermore, the effects of active tool-use on visuotactile interactions have often been compared directly with the effects of a passive condition where participants simply held the tool, or performed another task without using the tool. These passive control conditions leave open the possibility that any resulting effects are not specific to ‘tool-use’¹ per se, but rather to some form of target-directed motor activity alone. The choice of a suitable control condition is therefore of great importance in these and in future studies.

Several possible alternative hypotheses could equally well explain the majority of existing data arising from visuotactile studies of tool-use (i.e., the enhanced effects of visual stimuli presented at the tip of a tool on detection or discrimination of simultaneous tactile stimuli applied to the hand holding the same tool). First, while visual stimuli presented at the tips

of the tools may effectively interact with simultaneous tactile stimuli presented to the hands, visual stimuli presented near the hands or along the shaft of the tool may not show any such enhanced bimodal effectiveness during or following tool-use. This would suggest that, rather than *expanding* or *elongating* the VRFs of certain bimodal neurons along the tools, these VRFs are rather *projected* or *shifted* along the tools, with their centres now displaced to the tips of the tools. This hypothesis makes the following predictions: (1) Visuotactile interactions for bimodal stimuli presented on the same tool will be stronger than for visual and tactile stimuli presented on different tools, but only, or more strongly, at the tips of the tools, and not, or less strongly, near the hands or in the middles of the tools; and (2) The magnitude of visuotactile interactions will increase with increasing distance of the visual stimuli from the hands, reaching a maximum at the tips of the tools (see Fig. 1B).

A third possible hypothesis is that visuotactile interactions measured at the hands of the tool-user do not change in strength or in relative magnitude during or following tool-use, but that the region of space around the tips of the tools begins to display properties similar to those of peripersonal space near the hands. This hypothesis makes the following predictions: (1) The same-tool versus opposite-tools difference in visuotactile interactions will be stronger near the hands and at the tips of the tools, than in the middles of the shafts of the tools; and (2) The magnitude of visuotactile interactions will be largest at the hands, smallest in the middle of the tools, and larger again at the tips of the tools, perhaps even as large as for visual stimuli presented near the hands (see Fig. 1C). The null hypothesis, that tool-use has no effects on VRFs of bimodal neurons, is depicted in Fig. 1D.

A number of other hypotheses and predictions are also possible for the effects of tool-use on visuotactile interactions in peripersonal space. However, since visual stimuli have only ever been presented at the tips of tools in the existing human neuropsychological and experimental literature on tool-use, many such hypotheses could be equally applicable to the existing published data. The experimental hypotheses presented here are what we consider to be three of the most parsimonious accounts of the available data.

One important caveat, and an assumption central to the present work (and to many other visuotactile studies of tool-use) needs to be stated explicitly; Visuotactile peripersonal space, as defined in terms of body part-centred VRFs, can only be studied *directly* in single- or multi-unit studies of awake or anaesthetised macaque monkeys or other experimental animals. By contrast, the existing human experimental literature on tool-use and peripersonal space concerns the effects of visual stimuli presented in regions of space at different distances from a participant’s body, on the simultaneous detection or discrimination or tactile stimuli presented to the participant’s hand. There is no a priori reason to expect such performance, as indexed behaviourally by reaction time or error measurements, to be lawfully related to, and/or dependent upon, the typical properties of single bimodal neu-

¹ The definition of ‘tool-use’ that we prefer to use is that of Beck [1], who provided an exhaustive catalogue of different tool-use behaviours as observed in non-human animals, typically primates. According to Beck’s definition, “tool use is the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool.” (p. 10)

rons as recorded in macaque monkeys' premotor or posterior parietal cortices. Despite this methodological gap, the model of visuotactile peripersonal space seems to have become the dominant one within which to interpret the visuotactile consequences of tool-use [12,17,18]. This may be due to the influence of the oft-cited study of Iriki and colleagues [8], from which many later studies seem to have taken their inspiration, and where the question of tool-use and peripersonal space was first raised.² We have chosen to examine the visuotactile consequences of tool-use using a behavioural task in healthy human participants that seems to provide an index of common spatial location across sensory modalities (for reviews, see [7,23]). The extent to which this particular behavioural task relates to the single-cell properties of visuotactile peripersonal space in the macaque monkey is yet to be determined, and is an important issue for future research using converging methodologies. For the purposes of the present report, however, we assume that the crossmodal congruency task does indeed provide a reliable index of visuotactile integration in peripersonal space.

We measured the interaction between visual and tactile stimuli presented on two hand-held tools using the crossmodal congruency task [23] interleaved between a series of 'tool-use' trials. Seventy-two participants (24 per experiment; 69 right-handed, 3 left-handed by self-report; 43 female, 29 male, ages 18–45, mean age (\pm S.E.M.) 26.6 ± 0.6 years) discriminated the elevation of vibrotactile stimuli presented to either their thumb ('upper') or forefinger ('lower') of either hand, while trying to ignore random, irrelevant, and non-predictive visual distractors presented in either an upper or lower location on the same or opposite side with respect to the vibrotactile target. Responses were made using two-foot pedals, one under the toes ('upper'), and the other under the heel ('lower') of the left or right foot of the participants (counterbalanced). Trials in which the visual and vibrotactile stimuli were presented from the same elevation (i.e., both upper or both lower) were termed "congruent," and trials in which visual and vibrotactile stimuli were presented from different elevations were termed "incongruent". Congruency in the present experiments refers, therefore, to the congruence of the visual distractors with respect to the target vibrotactile stimuli, regardless of their relative sides of presentation (i.e., on either the same or opposite tools), and regardless of the distance of the visual distractors (i.e., on the handles, shafts, or tips of the tools).

² While Iriki et al. [9] interpreted their results primarily in terms of the subjective representation of the body (the 'body schema'), their methodology resembles somewhat the methodology of Graziano and colleagues (although there are significant differences—see [7]), who studied the *visuospatial* properties of premotor and parietal neurons representing peripersonal space (e.g., see [5]). Iriki et al. set out to measure the plastic changes of VRFs following tool-use by presenting the experimental animals with a moving visual stimulus (a small piece of food, which was also used to reward the animals during tool-use training). This approach seems more related to studies of the representation of peripersonal space than to that of the body schema. For a review and critical discussion of Iriki et al.'s work, see [7].

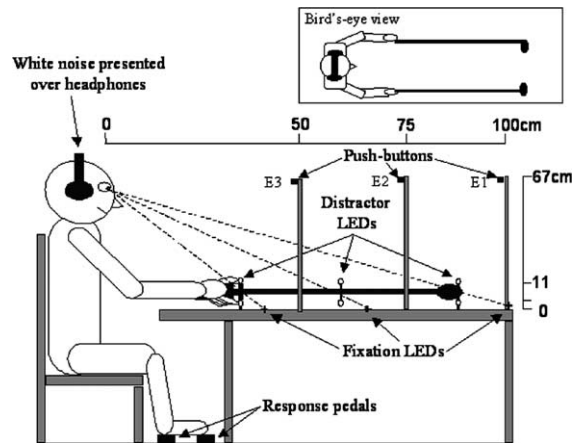


Fig. 2. Participants held a tool in both hands (see inset), and fixated one of three central fixation LEDs (depending on the visual distractor distance). Central fixation was monitored via a closed-circuit television system for eight participants in each experiment, and all were able to maintain central fixation reliably throughout the experiments. Visual distractors were presented from near the Handles, Shafts, or Tips of the tools in different blocks of trials, and from upper or lower elevations. Upper or lower elevation vibrotactile targets were presented simultaneously to the participants' hands on either side. Participants responded by lifting the front pedal for 'upper' targets and the rear pedal for 'lower' targets. After every fourth trial, participants used one tool to depress a button 100, 75, or 50 cm from the participant (labelled E1, E2, and E3, respectively).

In this primary crossmodal congruency task, visual distractors were presented at one of three distances along one of two tools, one held in either hand (see Fig. 2). During the crossmodal congruency task, participants maintained fixation on one of three central fixation LEDs, depending on the visual distractor distance (i.e., the block type). One visual distractor distance, and hence one corresponding fixation position, was tested in each block of trials. Each block type was run twice, and the order of the blocks was counterbalanced across participants according to twelve predetermined counterbalanced block orders under the constraints that each half of the experiment contained one block of each type, and that no two consecutive blocks were of the same type.

After every fourth trial of the crossmodal congruency task, participants used either the tip, the shaft, or the handle of one of the two tools to push a button (1 cm^2) located 45 cm above the tabletop and 100, 75, or 50 cm away from their body, respectively, in response to an LED that was illuminated randomly on either side indicating the appropriate tool to be used and target to reach toward. In these tool-use tasks, the participants pressed the target buttons with a screw that protruded 3 cm from the upper surface of the tools at the handles, midway along the shafts, and at the tips of both tools. Six further screws protruded 3 cm from the lower surface of the tools, below each of the upper screws. Participants were instructed to use only the upper screws to push the target buttons, and to push the buttons upward with the tool. This restriction ensured that the specific action performed by participants was controlled as far as possible between participants during the tool-use task.

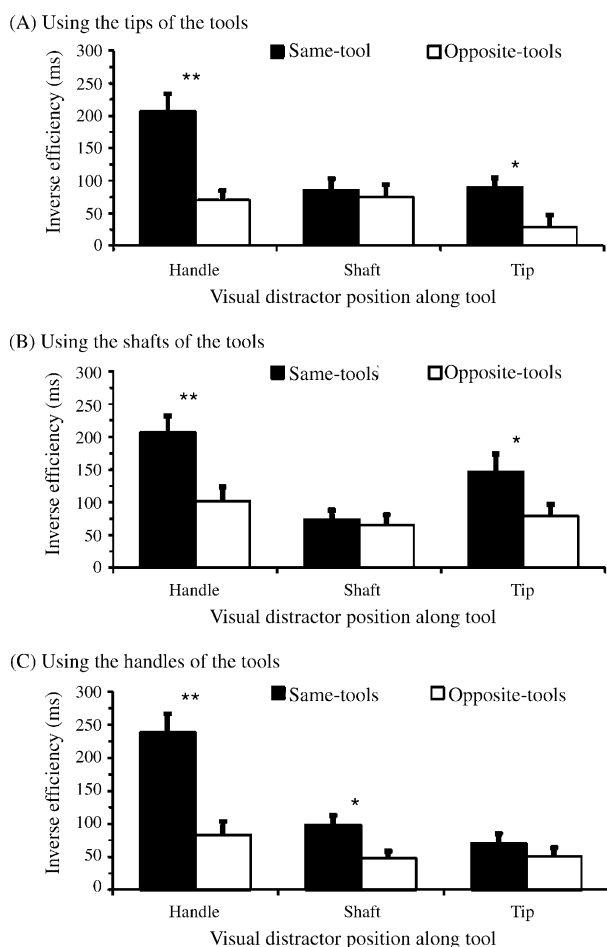


Fig. 3. Visuotactile interactions depend on the part of a tool being used. Bars show inverse efficiency (median RT/proportion correct responses [24], \pm S.E.M.) for 24 different participants per Experiment. (A) Experiment 1: When the tips of the tools were used to perform the tool-use task, visual distractors near the handles and near the tips resulted in a larger crossmodal congruency effect when presented with same-tool vibrotactile targets than with opposite-tool targets in interleaved trials of the crossmodal congruency task. (B) Experiment 2: The same pattern of visuotactile interactions occurred when the shaft of the tool was used. (C) Experiment 3: When the tool handle was used, the pattern of visuotactile interactions changed. * $p < .05$, ** $p < .01$, corrected for multiple comparisons.

Across all three experiments, the same tools were used, and the tools remained in an identical position, resting within four small tubes affixed to the table top, during the performance of the crossmodal congruency task. Any reliable differences between experiments can therefore be attributed to the effects of the intervening tool-use task on the spatial pattern of visuotactile interactions, rather than to any differences concerning the visual appearance, the weight, or length of the tools themselves.

All experiments were approved by the local research ethics committee, and were conducted in accordance with the declaration of Helsinki. In Experiment 1 (Fig. 3A), participants used the tips of either tool to push a button 100 cm away. In Experiments 2 and 3, different groups of participants used either the middle of the shaft of either tool (Fig. 3B) or the tool

handle (Fig. 3C) of either tool to push buttons located at 75 and 50 cm, respectively. The primary crossmodal congruency task was identical across all three experiments.

Incongruent visual distractors interfered significantly with participants' discrimination of vibrotactile targets at all distractor positions (the crossmodal congruency effect); however, the magnitude of this effect was modulated both by the relative positions of the distractors and by the interleaved tool-use task that participants performed. Across all three experiments, when the distractor and target stimuli were presented on the same tool (i.e., on the same side of space), crossmodal congruency effects were significantly larger than when the target and distractor stimuli were presented on opposite tools (significant main effect of distractor Tool, $F(1, 69) = 59.95$, $p < .001$). Similarly, visual distractors presented near the hands, in peripersonal space, resulted in the largest crossmodal congruency effects in all three experiments (significant main effect of distractor Distance, $F(2, 68) = 34.98$, $p < .001$). The interaction between these two factors was also significant ($F(2, 68) = 20.86$, $p < .001$), revealing that visual distractors presented on the same tool as the concurrent vibrotactile target resulted in significantly larger congruency effects, but that this 'same-tool' effect also depended on the distance of the visual distractor from the hands.

Finally, the nature of the interaction between Distance and Tool varied significantly between the three experiments (Distance–Tool–Experiment interaction, $F(4, 138) = 2.5$, $p < .05$). This three-way interaction revealed that the two-way interaction between Tool and Distance was modulated significantly by the parts of the tools used to perform the tool-use task. When participants manipulated the tips (Fig. 2A) or the shafts (Fig. 2B) of the tools, visual distractors presented both near the tips of the tools ('Tips') and near the hands ('Handle') interfered significantly more with vibrotactile targets presented on the same-tool than on opposite-tools. By contrast, visual distractors located on the shafts of the tools ('Shafts') interfered equally with tactile targets presented to either tool. When the secondary task involved manipulating the handles of the tools (Fig. 2C), the same- versus opposite-tool difference was observed only at the handles and on the shafts of the tools, and not at their tips.

Our results suggest that the use of tools may not simply 'extend' peripersonal space (see also [7] for further discussion), but rather that only the tips of the tools become behaviourally relevant to visuotactile interactions associated with the hand that holds the tool, as depicted in Fig. 1C. This seems to involve the highlighting of certain regions of space, or of the tools themselves, that are dependent upon the nature of recent and/or upcoming tool-use actions. This highlighting was particularly evident when participants used the tips (Fig. 2A) or the handles (Fig. 2C) of the tools. When the shafts of the tools were used, however (Fig. 2B), visual distractors on the shafts still did not show any preferential effect of one tool with respect to the other, while the distractors at the tips showed a strong effect. This result is surprising, since one might expect that when the shafts of the tools were used to

perform the intervening tool-use tasks, increased same-tool versus opposite-tools crossmodal congruency effects should be observed along the shaft. We discuss this finding in more detail below.

One intriguing possible explanation for the unexpected effect observed in Experiment 2, where participants used the shafts of the tools, comes from an analogy with the neural representation of the body itself. The joints of the body's segments and the distal ends of the body itself (e.g., the elbows and hands, respectively) are more important, at least in terms of their neural representation, and in sensorimotor behaviour (e.g., [20]), than the middle portions of body segments (such as the forearms). It could be, that when we use a distal part of a tool (i.e., the shaft or tip of the tool), the brain represents preferentially, in some respect relevant to the present studies, only the proximal and distal ends of the tool, and not the entire length of its shaft. Indeed, perhaps the simplest representation of a long, straight object, computationally speaking, might be to represent the spatial locations of the two ends, and not to represent explicitly the middle of the object.

One anecdotal piece of evidence from the present series of experiments is of relevance here. During the Tool–Handle task (Experiment 3), and only during this task, participants occasionally and accidentally banged the tips or shafts of the tools into the surrounding experimental apparatus. The only functionally relevant part of the tool in Experiment 3 was the handle immediately adjacent to the participants' thumbs. This observation suggests that participants were neglecting the control of the rest of the tool as it moved through space. By contrast, in the other two experiments, the shafts of the tools needed to be guided effectively and efficiently through the workspace to interact with their target buttons. This requirement may have led to the distal tips of the tools being just as relevant to the tasks in the Tool–Shaft as in the Tool–Tip experiments.

In Experiment 3, while participants were actively wielding the tool in order to perform the button-pushing task, their occasional lack of control of the whole tool suggests that this task may not really count as 'tool-use,' at least according to Beck's [1] definition which requires the "proper and effective orientation of the tool" (p. 10) to be classed as tool-use. The active button-pushing task of Experiment 3 was not therefore, strictly speaking, a tool-use task, since proper orientation and control of the whole tool was not necessary for task completion (the target button was within the participants' normal reach). In Experiments 1 and 2, accurate control of the tool was required for task completion (in the absence of the participants' locomotion toward the target). This difference between the tasks, and between the results of the experiments (recall that the significant three-way interaction appears to be due to a difference between Experiments 1 and 2 on one hand, and Experiment 3 on the other), therefore allows us to regard the results of Experiment 3 as a baseline measure of crossmodal congruency effects in the absence of tool-use proper, but in the presence of an active, frequent, and unpredictable

target-directed motor task interleaved between the trials of the vibrotactile discrimination task.

A second possible explanation for the finding of significant same-tools versus opposite-tools differences in distractor effectiveness only at the tips of the tools, and not in the middle of the shafts in Experiments 1 and 2 relates to the nature of the tool-use task that participants were asked to perform. In several previous tool-use studies (e.g., [3,8,15]), human participants, or macaque monkeys used rake-like tools to retrieve objects from extrapersonal space, bringing the target object toward the body. It is possible that this retrieval action might serve to highlight those portions of space that are functionally relevant to the task: i.e., the region of space between the tip of the tool and the hand—the middle of the shaft of the tool. A definitive reply to this possibility cannot be derived from the present data, but note that, in performing the tool-use tasks in the present experiments, the participants were required both to remove the tool from its location on the table, to reach outward and upward to push the target button, then to return the tool, moving inward and downward, back into the correct position on the tabletop. Given the primary conclusions of the present investigation, that the effects of tool-use on the visuotactile representation(s) of peripersonal space depend on the particular tasks performed, we accept that a target-retrieval form of tool-use may indeed highlight the regions of space near the middle of the tools, thus resulting in a genuine 'extension' or 'expansion' of peripersonal space. This possibility needs to be tested explicitly using the crossmodal congruency task, or some other test of visuotactile interactions in future research.

The finding that it is only the tips of the tools that participate in the modulation of visuotactile interactions during tool-use is reminiscent of the famous and much-quoted statement of Head and Holmes [6]. They noted, "... these 'schemata' [allow] ... the power of projecting our recognition of posture, movement and locality beyond the limits of our own bodies to the end of some instrument held in the hand ... a woman's power of localization may extend to the feather in her hat." (p. 188). Head and Holmes were likely, in turn, reminded of the idea of the 'eccentric projection' of sensations transduced by the nervous periphery, but relating to distant objects (e.g., [4,13,14,25]). While these anecdotal reports of such phenomena relating to tool-use are interesting in their own right, from a historical point of view, it is not clear to what extent the phenomena of 'eccentric projection,' 'double sensations,' 'distal attribution,' or the 'incorporation' of inanimate objects into the body schema(ta) may relate to the present issue. In the experiments reported here, we focused on the tool-use-dependent plasticity of the multisensory representation of peripersonal space, which is closely related to, but not the same as, the representation of the body itself.

An important issue in studies of the effects tool-use on visuotactile integration in peripersonal space is that of designing a control condition that contains as many of the sensory and motor aspects of the tool-use task, without itself involving 'tool-use'. Previous studies have included several

forms of control conditions, of the following general forms: (1) A passive condition, in which participants do not perform a tool-use task before or during measurement of visuotactile interactions (e.g., [19]); (2) A no-tool condition, where participants perform the visuotactile task in the absence of any tools held in the hand, or holding only the detached handle of the tool (e.g., [16]); or (3) An active, non ‘tool-use’ task, such as pointing or reaching and grasping with the hand toward the same targets as in the ‘tool-use’ condition (e.g., [3,8,15]).

In the present series of experiments, we chose to study three very similar tool-use tasks, varying only in the part of the tool used to complete the tool-use actions, and the region of space where that action was performed. This design allowed the same number, frequency, and approximate difficulty of tool-use actions to be controlled across experiments, thus decreasing any potential differential effects of active versus passive conditions, or of performing interleaved tool-use actions, on the crossmodal congruency effects themselves.

Tool-use represents a class of complex, sensorimotor behaviours, which probably cannot be ascribed to the functioning of any one particular region of the brain (see [10] for review of some of the neural bases of tool-use behaviours). The visuotactile representation of peripersonal space, on the other hand, may submit to such a neural definition. Neurons displaying bimodal, visuotactile responses with spatially overlapping receptive fields have been discovered in the putamen, premotor cortex, the intraparietal sulcus, and in the superior colliculus. Such cortical and subcortical areas probably play an important role in generating the visuotactile behavioural interactions reported in the present study. Such behavioural interactions may rely on a form of neural plasticity that is rapid, task-dependent, and transitory. This may set it apart from other forms of plasticity, such as the ‘invasion’ of deafferented areas of somatosensory cortex by neighbouring afferent inputs [11]. Despite these potentially related results, we feel that research into the plastic effects of tool-use, particularly on a neural level, is at too premature a stage to speculate on the possible neural mechanisms subserving such behavioural plasticity (though see [22] for a recent study addressing a related issue).

It should also be noted that demonstrating a simple, lawful relationship between behavioural effects on the one hand, and the properties of individual neurons, often recorded from anaesthetised animal subjects, on the other, may not be possible. Furthermore, the behavioural influences of attention, response-preparation, and stimulus-response compatibility for example, may be of relevance to the literature on the visuotactile consequences of tool-use [9,21]. These issues are currently being addressed in our laboratory, using both behavioural and neuroimaging techniques.

Acknowledgements

N.P.H. is supported by a Wellcome Prize Studentship (number 065696/Z/01/A) from The Wellcome Trust. G.A.C. is supported by a Career Development Award from The Well-

come Trust. Many thanks to Charles Jones and to Angelo Maravita for commenting on earlier drafts of the manuscript.

References

- [1] B.B. Beck, *Animal Tool Behaviour: The Use and Manufacture of Tools by Animals*, Garland Press, London, 1980.
- [2] A. Berti, F. Frassinetti, When far becomes near: remapping of space by tool-use, *J. Cogn. Neurosci.* 12 (2000) 415–420.
- [3] A. Farnè, E. Lådavas, Dynamic size-change of hand peripersonal space following tool use, *NeuroReport* 11 (2000) 1645–1649.
- [4] J.J. Gibson, *The Senses Considered as Perceptual Systems*, George Allen & Unwin Ltd., New York, 1966.
- [5] M.S.A. Graziano, X.T. Hu, C.G. Gross, Visuospatial properties of ventral premotor cortex, *J. Neurophys.* 77 (1997) 2268–2292.
- [6] H. Head, H.G. Holmes, Sensory disturbances from cerebral lesions, *Brain* 34 (1911/1912) 102–254.
- [7] N.P. Holmes, C. Spence, The body schema and the multisensory representation(s) of peripersonal space, *Cogn. Process.* 5 (2004) 94–105.
- [8] A. Iriki, M. Tanaka, Y. Iwamura, Coding of modified body schema during tool use by macaque postcentral neurons, *NeuroReport* 7 (1996) 2325–2330.
- [9] A. Iriki, M. Tanaka, Y. Iwamura, Attention-induced neuronal activity in the monkey somatosensory cortex revealed by pupillometrics, *Neurosci. Res.* 25 (1996) 173–181.
- [10] S.H. Johnson-Frey, The neural bases of complex tool use in humans, *Trends Cogn. Sci.* 8 (2004) 71–78.
- [11] J.H. Kaas, Plasticity of sensory and motor maps in adult mammals, *Ann. Rev. Neurosci.* 14 (1991) 137–167.
- [12] E. Lådavas, Functional and dynamic properties of visual peripersonal space, *Trends Cogn. Sci.* 6 (2002) 17–22.
- [13] J.M. Loomis, Distal attribution and presence, *Presence* 1 (1993) 119.
- [14] R.H. Lotze, *Microcosmos: An Essay Concerning Man and His Relation to the World*, T & T Clark, Edinburgh, 1854/1885.
- [15] A. Maravita, K. Clarke, M. Husain, J. Driver, Active tool-use with contralesional hand can reduce crossmodal extinction of touch on that hand, *Neurocase* 8 (2002) 411–416.
- [16] A. Maravita, M. Husain, K. Clarke, J. Driver, Reaching with a tool extends visual-tactile interactions into far space: evidence from cross-modal extinction, *Neuropsychologia* 39 (2001) 580–585.
- [17] A. Maravita, A. Iriki, Tools for the body (schema), *Trends Cogn. Sci.* 8 (2004) 79–86.
- [18] A. Maravita, C. Spence, J. Driver, Multisensory integration and the body schema: close to hand and within reach, *Curr. Biol.* 13 (2003) R531–R539.
- [19] A. Maravita, C. Spence, S. Kennett, J. Driver, Tool-use changes multimodal spatial interactions between vision and touch in normal humans, *Cognition* 83 (2002) 25–34.
- [20] W. Penfield, E. Boldrey, Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation, *Brain* 60 (1937) 389–443.
- [21] L. Riggio, L. Gawryszewski, C. Umiltà, What is crossed in the crossed-hand effects? *Acta Psychol.* 62 (1986) 89–100.
- [22] M. Schaefer, Y. Rothmund, S. Rothmund, M. Rotte, Short-term plasticity of the primary somatosensory cortex during tool use, *NeuroReport* 15 (2004) 1293–1297.
- [23] C. Spence, F. Pavani, A. Maravita, N.P. Holmes, Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task, *J. Physiol.* (Paris) (in press).
- [24] J.T. Townsend, F.G. Ashby, *Stochastic Modelling of Elementary Psychological Processes*, Cambridge University Press, New York, 1983.
- [25] E.H. Weber, Tastsinn und Gemeingefühl [On the sense of touch and ‘common sensibility’], in: H.E. Ross, D.J. Murray (Eds.), *E. H. Weber on the Tactile Senses*, Earlbaum, UK, Taylor & Francis, Hove, 1846/1996, pp. 141–148.