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Action influences spatial perception: Neuropsychological evidence

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We present neuropsychological evidence indicating that action influences spatial perception. First, we review evidence indicating that actions using a tool can modulate unilateral visual neglect and extinction, where patients are unaware of stimuli presented on one side of space. We show that, at least for some patients, modulation comes about through a combination of visual and motor cueing of attention to the affected side (Experiment 1). Subsequently, we review evidence that action-relations between stimuli reduce visual extinction; there is less extinction when stimuli fall in the correct colocations for action relative to when they fall in the incorrect relations for action and relative to when stimuli are just associatively related. Finally, we demonstrate that action relations between stimuli can also influence the binding of objects to space, in a patient with Balint's syndrome (Experiment 2). These neuropsychological data indicate that perception–action couplings can be crucial to our conscious representation of space.

SEPARATE REPRESENTATIONS FOR PERCEPTION AND ACTION?

Over the last 10 years or so, a major distinction has been drawn between the coding of visual information for conscious perceptual judgements, on the one hand, and, on the other, the nonconscious coding of visual information for online action (e.g., see Milner & Goodale, 1995; Rossetti & Pisella, 2002, for reviews). For example, normal participants can be more susceptible to illusions when making perceptual judgements than when acting on stimuli, suggesting some dissociation between perceptual judgements and action (Aglioti, DeSouza, & Goodale, 1995; Bridgeman, 2002; Haffenden & Goodale, 1998; though for

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alternative views see Franz et al., 2000; Pavani, Boscagli, Benvenuti, Ratbuffetti, & Farne, 1999). This is further supported by data from neuropsychology. Damage to areas of ventral cortex can create severe problems in object recognition (visual agnosia), with even simple perceptual judgements being affected in some cases. Nevertheless, agnosic patients may still be able to make normal prehensile actions to the objects they fail to recognize (e.g., reaching and grasping). Perhaps the most well-known example of this is patient DF (Milner et al., 1991), who was unable to make orientation judgements to lines but remained able to orient a letter correctly when posting it through a slot. Here there is a dissociation between conscious perceptual judgements of a perceptual property (line orientation), whilst the same property can be used by visuomotor systems involved in controlling online action. The opposite dissociation can be observed in the syndrome of optic ataxia following damage to posterior parietal cortex. Here there can be relatively preserved object recognition, but poor reaching and grasping of objects (Perenin & Vighetto, 1988). In this instance, there is impaired visuomotor coupling although visual information is still available to support object recognition. The strong interpretation of such data is that there is independent coding of different visual representations, serving conscious perceptual judgements and object recognition on the one hand, and online action on the other (Milner & Goodale, 1995).

One problem for the argument that there are distinct perception and action systems is to explain how the different processes might communicate—as when we reach to a particular object because we recognize it as our own. However, the problem of communication might be less extreme than first appears, because perception and action systems may normally operate in a coupled manner. Here we must remember that although dissociations between tasks are useful for understanding structural constraints on information processing, they do not necessarily tell us about how processing normally operates. For example, although lesioning may separate two systems, in normality the processes involved may interact, and this interaction may be disrupted, when one of the contributing systems is impaired. Studies that address the interaction between perception and action in neuropsychological patients can thus be as informative for understanding normal function as studies of dissociations between processes in patients. It is interesting to note, then, that there is mounting evidence that perception and action interact—so that, e.g., perception is affected by action. For example, in an elegant series of studies Deubel, Schneider, and colleagues (e.g., Deubel & Schneider, 1996; Deubel, Schneider, & Paprotta, 1998; Schneider & Deubel, 2002) have shown that identification of a visual stimulus is improved when we point to the location where it appears, relative to when we point to another neighbouring location. This appears to be a necessary coupling. Deubel and Schneider demonstrate that a benefit from pointing to a target's location occurs even when the target is always presented at one location. This last result is informative because, if perceptual selection could be insulated from effects of action, then we ought to select the known target location independent of where an action is being directed. We do not seem able to do this.

Other researchers have shown effects from actions that seem to be activated implicitly, even when on overt response to a stimulus is not required. For example, Ellis and Tucker have reported that perceptual judgements (such as whether stimuli are inverted or not) are affected by both the position of the handle of an object with respect to the effector used for the response and by the compatability between the habitual response to the object and the response required in the task (fine vs power-grip) (Ellis & Tucker, 2000; Tucker & Ellis, 1998, 2001; though see Phillips & Ward, 2002). This suggests that perception can be influenced by action-related properties of objects. These action-related properties may be present in the image (e.g., whether a handle faces towards or away from the observer, which may determine the degree to which an object ‘‘affords’’ a particular action; cf. Gibson, 1979), or they may be based on associations with objects (see Yoon, Humphreys, & Heinke, 2002).

It is noteworthy that these last results come from studies of normal participants (presumably with intact visuomotor systems), whereas some of the strongest evidence for the independence of conscious perception and action comes from neuropsychology (e.g., Milner & Goodale, 1995). Is this inevitably the case? We believe the answer to this is no. In this paper we review recent neuropsychological data from our laboratory that show that perception can be strongly affected by action, supporting an interactive account of the processes involved. The paper is organized into two sections. First, we consider data showing that tool use can modulate visual extinction and neglect. Second, we present evidence on implicit action relation between stimuli. Extending prior work on effects of implicit action relations (Riddoch, Humphreys, Edwards, Baker, & Willson, 2003), we demonstrate that action-relations between objects not only facilitate conscious report of the stimuli but they also help to ‘‘bind’’ the stimuli to their locations. Overall, the results indicate that our perception of space can be influenced both by actions made towards objects and by action-related properties present in stimuli—in some cases, patients are poor at discriminating the locations of stimuli unless the stimuli fall in appropriate colocations for action.

EFFECTS OF TOOL USE AND VISUOMOTOR CUEING ON NEGLECT AND EXTINCTION

We begin by considering recent evidence on the effects of tool use on extinction and neglect. Extinction and neglect are relatively frequent consequences of damage particularly to the right hemisphere, classically being associated with damage to the right parietal lobe (Critchley, 1966). Patients with neglect may fail to respond to stimuli presented on the side of space contralateral to their lesion. Patients with extinction can respond to a stimulus presented on the contralesional side, but then fail to detect the same stimulus if another item is presented at the same time on the ipsilesional side. In both disorders, patients appear to be unaware of stimuli on the contralesional side of space, or even of that part of space altogether (see Baylis, Gore, Rodriguez, & Shisler, 2002).

Interest in the effects of tool use on neglect and extinction was first kindled by neurophysiological evidence. Graziano and Gross (1993; Graziano, 2002) reported cells in the putamen, areas 6 and 7 and the ventral intraparietal sulcus that respond to the simultaneous presentation of visual and tactile inputs. These cells are activated when visual stimuli fall in the vicinity of the relevant part of the body (e.g., the arm of the monkey), irrespective of the position of the body part in space, and they may play a role in representing stimuli in body part-centred coordinates (Graziano & Gross, 1998). Iriki, Tanaka, and Iwamura (1996) have further shown that a body-centred representation of space can be modified by tool use. Iriki et al. trained monkeys to retrieve food by using a rake-shaped tool. Following practice with the tool, visual stimuli in the vicinity of the tool activated cells normally sensitive to joint visual and tactile input near to the body (cf. Graziano & Gross, 1993). Apparently the body-centred representation had extended to incorporate the tool. The effect quickly dissipated once the monkey stopped using the tool.

Berti and Frassinetti (2000) first examined the effect of tool use in human subjects with neglect. They reported a patient whose neglect was most severe for stimuli presented close to his body, relative to when stimuli appeared further away (see also Halligan & Marshall, 1991). However, neglect became apparent even when stimuli were presented away from his body if the patient responded using a tool that extended into ‘‘far’’ space. Berti and Frassinetti propose that tool use had the effect of extending the patient’s (impaired) representation of ‘‘near’’ space to what was formerly ‘‘far’’ space, so that there was then neglect of stimuli in those locations.

Other investigators have shown effects of tool use on extinction. For example, Farnè and Ladavas (2000) examined cross-modal extinction, with visual stimuli presented on the ipsilesional side and tactile stimuli on the contralesional side (see also Maravita, Husain, Clarke, & Driver, 2001). There was relatively little extinction when the visual stimulus was presented away from the ipsilesional hand. This suggests that a distant visual stimulus was not coded in the patient’s representation of ‘‘near space’’, so that it did not compete with the tactile stimuli presented on the contralesional side of this space. After this, the patients practised retrieving objects using a tool with their ipsilesional hand before being tested again for cross-modal extinction (but this time holding the tool with their ipsilesional hand). The visual stimulus was presented in the same location as before, but now it fell close to the end of the tool. Farnè and Ladavas (2000) found that there was increased cross-modal extinction produced by a visual stimulus close to the tool on the ipsilesional side, when they assessed the patients' ability to detect a tactile stimulus on the contralesional side.

A somewhat different pattern of results was reported by Maravita, Clarke, Husain, and Driver (2002). They trained a patient to use a tool with his contralesional limb to move stimuli on the ipsilesional side. Here tool use may lead to the limb being linked to an intact representation of space on the ipsilesional side. Consistent with this, there was reduced extinction of a tactile stimulus presented on the contralesional limb by an ipsilesional visual stimulus. This benefit from tool use lasted up to 90 min after practice in using the tool.

In the above cases, the patients appeared to suffer from neglect or extinction within ''near space'', close to the body. In contrast to this, we have examined effects of tool use in a patient who showed greater neglect of far relative to near space (Ackroyd, Riddoch, Humphreys, & Townsend, 2002). Our patient, HB, was impaired at detecting stimuli not only on his contralesional (left) side but also stimuli on his ipsilesional side, if the ipsilesional stimuli fell away rather than close to his body. This problem was linked to the visual locations of stimuli and could not be attributed simply to poor intentional movement to the affected side.[1] We had HB try to detect stimuli when he held a stick in front of him. Under these circumstances HB's neglect of stimuli in far, ipsilesional locations improved, though there was little benefit in detecting stimuli on the contralesional side. However, if the stick was held at 90° pointing to the left then HB began to detect stimuli on the contralesional side, whereas detection of far, ipsilesional stimuli dropped. The contrasting effects when the stick was held straight ahead or 90° to the left show that any benefit was not due to some nonspatial factor, such as increased arousal. Instead, HB appeared to be aware of stimuli that fell close to the end of the stick he was holding (in far ipsilesional locations when the stick was held straight ahead; in contralesional locations when the stick was held to the left), as if the stick were extending his conscious perception of visual space.

There are various ways that we can think about these effects of tool use on neglect and extinction. One view is that holding and using a stick leads to a remapping of ''near'' space so that it encompasses locations around the stick as well as the body. In a patient with a neglected representation of ''near'' space, holding the stick leads to this impaired representation being extended to positions distant from the body (cf. Berti & Frassinetti, 2000). In a patient with a

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[1] This was demonstrated in tests of HB's ability to cancel lines on a page under free vision and when he viewed the stimulus through a mirror. Under free visual conditions, he omitted lines on the left side of the page, typically failing to move his hand to that part of space. In contrast, under mirror viewing conditions, he cancelled lines further to the left of the page and omitted lines on the right (which fell on the left side of visual space). Thus HB had poor awareness of left and far positions in visual space.

neglected representation of far space, holding the stick leads to the more intact representation of ‘‘near’’ space being remapped to the formerly impaired spatial positions (Ackroyd et al., 2002). However, another possibility is that, at least where neglect is improved, tool use provides a cue from the motor system to visual attention, so that the patient begins to attend to the affected part of space. Through attention to the cued locations, the patient may become aware of neglected spatial positions.

To test these different possibilities, we have recently extended our study of the effects of tool use in neglect to include a second patient, MP. MP has previously been documented in several papers (Edwards & Humphreys, 1999; Humphreys & Riddoch, 2001, 2002). One interesting aspect of his neglect is that it is sensitive to action properties of objects. Humphreys and Riddoch (2001) had MP perform simple visual search tasks using common objects, with the target being defined either by its name or by an action (e.g., ‘‘find the object you would drink from’’). They found that MP showed less neglect when cued by the action than when he was cued with the object’s name, even though individual objects could be named when presented directly in front of him. This advantage for cueing search by action was most pronounced when the objects were oriented with their handles turned towards MP’s body, so that the objects ‘‘afforded’’ the cued action. Humphreys and Riddoch proposed that MP was better able to sustain and use a ‘‘memory template’’ for action, rather than a template based on the object’s name, and this guided his search towards a matching target. This finding fits with the idea that action-related properties of stimuli in the environment can influence attention and conscious awareness of space, a theme we return to later.

As we will demonstrate in Experiment 1 (below), MP shows more pronounced neglect of stimuli in ‘‘near space’’, close to his body, than to stimuli in ‘‘far space’’, away from his body. This provides us with the opportunity to test whether tool use affected spatial mapping or attentional cueing, in his case. We had MP carry out a series of search tasks for targets defined by their names. There were seven search conditions, separated into four sets:

1. In the baseline condition, MP simply held his ipsilesional hand by his side during search.
2. In the ‘‘stick’’ conditions, he either held a stick out in front of him with his arm outstretched (‘‘horizontal stick’’ condition) or he held the stick vertically, again with his arm outstretched (‘‘vertical stick’’ condition). Only in the ‘‘horizontal stick’’ condition should search be affected by any remapping of near space to the space around the stick—as with Berti and Frassinetti’s (2000) patient, we might expect such remapping to worsen performance in ‘‘far’’ space for a patient showing neglect of ‘‘near’’ space. When the stick was held vertically, any spatial remapping should be irrelevant to search since the end of the stick did not fall close to the objects.

3. These ‘‘stick’’ conditions were matched to two ‘‘arm’’ conditions, in which MP searched either with his arm stretched out in front of him (‘‘horizontal arm’’) or with his arm held in a vertical upright manner (‘‘vertical arm’’). The ‘‘arm’’ conditions control for any effects of visuomotor cueing and arousal. In both of the ‘‘stick’’ conditions, the stick may serve as a visual and a motor cue to the region of space that MP was pointing to, based on movements of his outstretched arm. The ‘‘horizontal arm’’ condition may provide a similar visuomotor cue. The ‘‘vertical arm’’ condition contrasts with this. This condition should be as arousing as the ‘‘horizontal arm’’ condition (perhaps even more so, given the effort required to hold one’s arm in a vertical position), but it should not provide a visuomotor cue to the space being searched. If visuomotor cueing is important, then there should be reduced (not increased) neglect in the cases where MP searched with his arm outstretched (both ‘‘stick’’ conditions and the ‘‘horizontal arm’’ condition), relative to the ‘‘vertical arm’’ and baseline treatments.

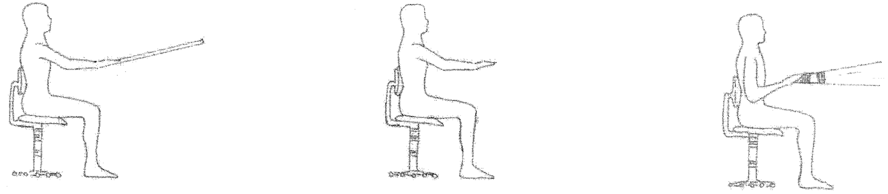
4. The final two conditions were included to provide either a visual cue alone (with no motor component from MP holding his arm outstretched) or a motor cue alone. In the visual cue condition, MP searched using a torch held with his ipsilesional hand to point consecutively to objects, but with his hand held by his side. In the motor cue condition, MP’s arm was covered by a cloth. He moved the arm under the cloth whilst he searched but he could not see his arm movements. If MP’s performance was best when he could both move and see his arm, the evidence would suggest positive effects of combined visual and motor (action) cueing on neglect. Examples of the conditions are shown in Figure 1.

EXPERIMENT 1: TOOL USE IN A PATIENT WITH NEGLECT OF ‘‘NEAR SPACE’’

Method

MP, a left-handed former toolmaker and fitter, was 55 at the time of testing. In 1992 he suffered a middle right artery occlusion and infarct that damaged the right frontoparietaltemporal junction, including the superior and inferior frontal gyri, the superior temporal gyrus, and the postcentral gyrus. He had a hemiparalysis of his contralesional upper limb. On standardized tests, such as line bisection, MP shows left neglect, and he typically misses targets in the bottom left quadrant on star cancellation. Verbal intelligence assessed by the NART predicted a full scale IQ of 90. Prior details of MP’s case, and details of an MRI scan, are presented in Edwards and Humphreys (1999) and Humphreys and Riddoch (2001).

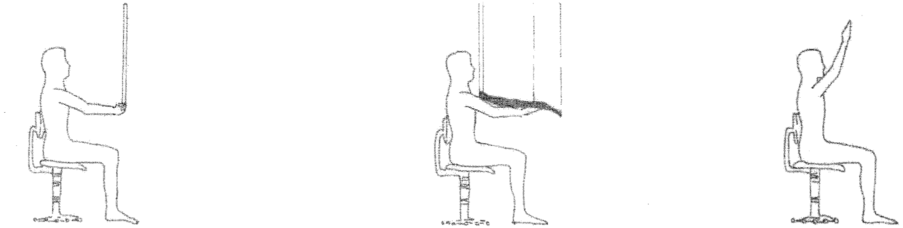
In each condition MP was presented with nine common objects on a table in front of him, with the objects covering an area of 1.44 m^2. The objects appeared in three lateral locations (centred on his body or 80 cm left or right) and at three distances from MP (30, 75, and 120 cm). The experiment was based on blocks of



Horizontal stick: MP was asked to perform the search task holding the stick out in front of him.

Horizontal arm: MP was asked to perform the search task holding his arm out in front of him.

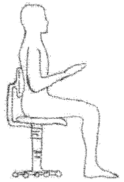
Vision only: MP was asked to use the torch to guide his search and to keep his arm close to his body (within about 15 cm).



Vertical stick: MP held a stick in a vertical position, with his arm outstretched, as he searched.

Motor only: MP was asked to act exactly as in the horizontal arm condition, but a plastic cloth was put in front of him covering the extent of his arm at full stretch. This enabled him to see the objects but not his arm as it moved.

Vertical arm: MP was asked to maintain his ipsilesional arm straight above his head while searching for the objects.



Baseline

Figure 1. The experimental conditions used with patient MP in Experiment 1.

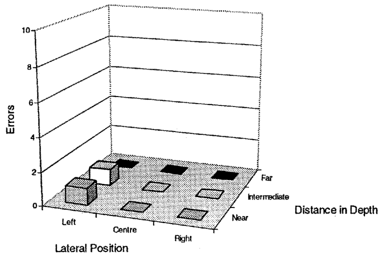
nine trials, during which the set of objects in front of MP remained constant. Across a trial block, each object was named once as a target, with the objects chosen in a random order (ensuring random sampling of the nine locations). Within each block, the nine objects were drawn at random from a total set of sixty-two common objects, with the objects ranging in size from a stamp (7.5 × 8.5 cm) to a kettle (20 × 23 × 13 cm). The objects for a block were randomly assigned to each of the nine locations. Each condition was based on 10 blocks of trials.

For each condition, MP was given the name of a target at the start of each trial and he had to point to the target once he located it. Across a trial block he was given 12 names—9 names of targets (actually present) and 3 of nontargets (that were not present on the table). The nontarget names corresponded to objects from the total set of 62 objects sampled across the study. On trials where MP neglected the target, search could be quite prolonged. To limit this, we took as a cut-off a search time of 20 s. Note that control participants can perform the search task effortlessly within this time. In the ''stick'' conditions, MP held a thin white stick 60 cm long and 60 g in weight in his ipsilesional hand. He was asked to hold his ipsilesional arm outstretched in these conditions, and he was allowed to move his arm as he searched for a target. In the ''horizontal arm'' and ''motor only'' conditions, his arm was held as in the ''stick'' conditions and he was allowed to move it during search. However, in the ''motor only'' condition a plastic cloth was suspended at shoulder height from the ceiling, so that MP could not see his arm as it was moved. In the ''vertical arm'' condition, MP was asked to hold his arm in a vertical position during each trial, lowering it in between trials. In the ''vision only'' condition MP held a small torch in his ipsilesional hand, but this was held at his side. He was allowed to shine the torch on each object during search. In the baseline, search was conducted with both hands by his side. The trial blocks were conducted in a random order across the search conditions.

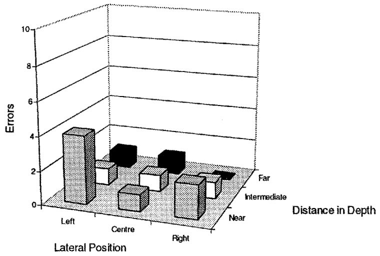
Results

We analysed the number of ''misses'' made by MP, where he failed to detect the target within the search period. There were no false alarms (when a nontarget name was cued). There were insufficient data to analyse the effects of lateral position and depth together, though it was evident that MP typically missed most targets in the ''near left'' location, though some targets in the right locations were also occasionally missed. Figure 2 shows the number of misses in each of the nine locations, for each of the search conditions. Overall accuracy was affected by both lateral position, $\chi^2(2) = 36.99$, $p < .001$, and distance, $\chi^2(2) = 30.24$, $p < .001$.

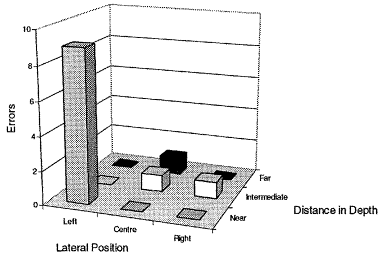
The percentage of misses within each condition, averaged across the positions, is given in Figure 2. Statistical comparisons between the conditions are



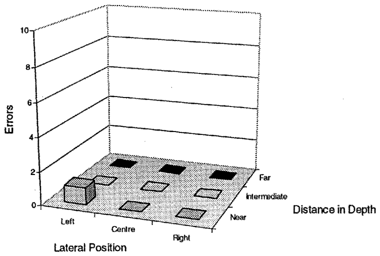
Horizontal stick



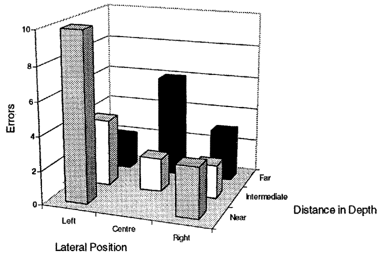
Horizontal arm



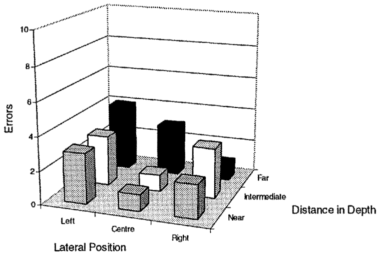
Vision only (torch)



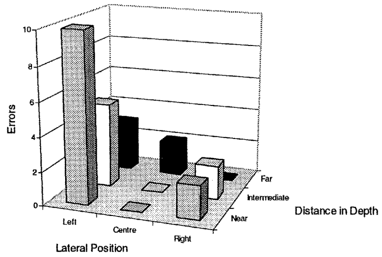
Vertical stick



Motor only (arm covered)



Vertical arm



Baseline

Figure 2. The number of misses ($N = 10$) made by patient MP for each stimulus location in each condition, in Experiment 1.

presented in Table 1. Relative to the baseline condition, there was a benefit when a visual cue was present to guide search (in both ''stick'' conditions, with the ''arm horizontal'' and with the ''vision only'' [torch] conditions). Performance did not differ from the baseline in the ''vertical arm'' and ''motor only'' conditions (in fact there was a trend for performance to be worse than the baseline in the ''motor only'' condition). In addition, the presence of a strong motor cue (holding the stick) improved performance relative to when this strong cue was absent (''arm horizontal'' and ''vision only'').

Discussion

These results do not fit at all with the idea that tool use affects neglect by remapping space near the body to the space around the tool. MP showed neglect of ''near'' relative to ''far'' space (Figure 2). If a remapping effect had taken place, we would expect MP to show greater, not less, neglect when he searched for objects with a stick held in front of him. Instead of this, tool use improved his performance. The other search conditions provide some indications as to how this beneficial effect came about. In particular, relative to the baseline, MP manifested less neglect when there was a visual cue present to guide his search—when he shone a torch onto objects and when he searched with his ipsilesional arm outstretched (the ''stick'' and the ''horizontal arm'' conditions). The benefit was strongest when he held a stick as he pointed. This is unlikely to be due to an increase in arousal alone, since there was minimal effect when MP held his ipislesional arm in a vertical position during search, although this was an effortful action. We conclude that a motor cue, from holding the stick, combined with a visual cue, his outstretched arm, improved the allocation of attention to space. This may be thought of in similar terms to the findings of Deubel, Schneider, and colleagues (Schneider & Deubel, 2002) where motor actions, perhaps combined with visual cues, enhance attention and detection at the location for which an action is programmed. In the present instance MP failed to notice some parts of space (neglecting the objects that fell there) unless visual and motor cues combined to draw his attention there.

Although we attribute these effects with MP to visuomotor cueing, we do not think that all effects of tool use come about in this manner. Consider the data of Maravita et al. (2002), where cross-modal extinction was reduced when the patient used a tool with the contralesional hand, but on the ipsilesional sided of space. It is hard to see why any visuomotor cue to the ipsilesional side should improve performance. On the other hand, an improvement could come about if the contralesional limb is remapped into an intact representation of space, by moving the tool within that region. From this we conclude that effects of tool use may come about in a number of ways—in some cases through spatial remapping, in other through visuomotor cueing of attention. Potentially important factors here might be whether the patient has experience in using the implement

TABLE 1
χ^2 tests between the conditions in Experiment 1

	Motor only	*Baseline*	*Arm vertical*	*Light torch*	*Arm horizontal*	*Stick horizontal*	*Stick vertical*
Motor only	—	$\chi^2(1) = 3.41$ n.s.	$\chi^2(1) = 5.48$ $p < .05$	$\chi^2(1) = 15.70$ $p < .001$	$\chi^2(1) = 15.70$ $p < .001$	$\chi^2(1) = 37.78$ $p < .001$	$\chi^2(1) = 40.95$ $p < .001$
Baseline		—	$\chi^2(1) = 0.27$ n.s.	$\chi^2(1) = 5.00$ $p < .05$	$\chi^2(1) = 5.00$ $p < .05$	$\chi^2(1) = 21.76$ $p < .001$	$\chi^2(1) = 24.57$ $p < .001$
Arm vertical			—	$\chi^2(1) = 3.01$ n.s.	$\chi^2(1) = 3.01$ n.s.	$\chi^2(1) = 17.99$ $p < .001$	$\chi^2(1) = 20.71$ $p < .001$
Light torch				—	$\chi^2(1) = 1$ n.s.	$\chi^2(1) = 7.75$ $p < .01$	$\chi^2(1) = 10.03$ $p < .01$
Arm horizontal					—	$\chi^2(1) = 7.75$ $p < .01$	$\chi^2(1) = 10.03$ $p < .01$
Stick horizontal						—	$\chi^2(1) = 0.34$ n.s.
Stick vertical							—

as a tool prior to the experimental task. In the primate work of Iriki et al. (1996) there is some indication that experience of using the implement as a tool might be important for remapping; there was remapping of the receptive fields of the critical cells only when the monkeys had experience in manipulating a stick for a reward. MP did not have experience of using the stick as a tool, and hence it may have served only as an attentional cue. In addition, the distances of the objects from MP's body were in all cases somewhat closer than those used by Berti and Frassinetti (2000). Again, this might encourage the use of the stick as an attentional cue rather than as the medium for remapping space. For our present purposes, the important point is that (either way) action-based effects, through tool use, moderate conscious awareness of space.

ACTION RELATIONS AFFECT PERCEPTUAL SELECTION IN VISUAL EXTINCTION

There is strong neuropsychological evidence that perceptual selection is influenced by factors that affect object recognition—such as whether visual elements group on the basis of a Gestalt property (e.g., continuation, collinearity, common motion, etc.), whether they form a known object, or whether separate objects are associatively related. The syndrome of visual extinction is again relevant here. In several studies it has been shown that extinction can decrease if the contra- and ipsilesional stimuli group by continuation, collinearity, common enclosure, common shape, and contrast polarity (e.g., Gilchrist, Humphreys, & Riddoch, 1996; Humphreys, 1998; Mattingley, Davis, & Driver, 1997; Ward, Goodrich, & Driver, 1994). Even without the aid of low-level Gestalt factors, extinction can be reduced if stimuli are parts of a known object (e.g., if two letters form a word rather than a nonword; Kumada & Humphreys, 2001). It can also be reduced if two stimuli are associatively related to one another (e.g., with two associated words; see Coslett & Saffran, 1991). These effects of low-level and knowledge-based (stored unit and associative) grouping may reflect reduced competition between stimuli during the recognition process; when stimuli group, this competition for recognition is reduced (see Heinke & Humphreys, 2003, for an explicit model). The evidence in addition suggests that such grouping processes may operate preattentively, so that conscious awareness of the stimuli is contingent on the appropriate grouping relations being present.

Recently, Riddoch et al. (2003) reported evidence that extinction is also affected by action relations between stimuli (e.g., whether or not two stimuli are in the appropriate locations to be used together). These effects come about even when the stimuli do not group through low-level Gestalt factors, and they are not contingent on associative relationships between objects. These results indicate that perception can be influenced not only by explicit action (see earlier), but also by implicit action relations between objects in the environment. Riddoch et al. (2003) tested five patients, three with unilateral right parietal damage (JB, MB, MP), one with unilateral left parietal damage (RH) and one with bilateral parietal damage, more pronounced on the right than left (GK). All the patients showed spatial extinction, with items on the contralesional side of space being difficult to identify when other items appeared simultaneously on the ipsilesional side.[2] A first study assessed the identification of pairs of objects that were commonly used together, with the objects either being placed in the correct spatial locations for actions (e.g., a corkscrew going into the top of a wine bottle) or in incorrect spatial locations for action (the corkscrew going into the bottom of the bottle; see Figure 3a). In both the correct and incorrect location conditions, the pairs were presented twice, with each object appearing once in each field. There were also single object trials in which each individual stimulus was exposed in the same location as it appeared in the trials with two objects. Stimulus exposure times were adjusted for individual patients so that they were able to identify about 80% of the single objects on the contralesional side (Figure 4a).

On trials where two objects appeared, identification of both objects was improved if the stimuli were placed in the correct positions for action relative to when they were placed in incorrect positions for action (Figure 4b). This held for all of the patients. There are several reasons for arguing that the effect was not due to guessing. First, the same objects were used in the correct and incorrect location conditions, so the chances of guessing the identity of the contralesional item from the ipsilesional one should have been equal irrespective of whether the spatial relations were appropriate for action. Second, the errors on two-object trials for two patients (MP and GK) typically involved them reporting that only an ipsilesional item was present—they never made errors on single item trials by guessing the identity of a second object. Since a guessing account is unlikely, it appears that action relations affected perception. Perception of both objects improved if they fell in the correct positions for action relative to when they were in incorrect positions.

Riddoch et al. (2003) also examined the performance of the patients when they only reported one of the two objects present in a pair. The objects in each pair were assigned to one or two categories. The ‘‘active’’ partner was the object that was moved when the action was performed; the ‘‘passive’’ partner was the object that was stationary during the action. In the example given above, the corkscrew was categorized as the active partner and the wine bottle as the passive partner. A clear difference emerged between the identification of the active and passive partners, on trials where only one member of an object pair was reported. In the correct location condition, the active member of a pair

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[2] For GK, we class his left side as contralesional and his right as ipsilesional, even though he has bilateral lesions, since the damage is more extensive within his right hemisphere and he shows left-side extinction.

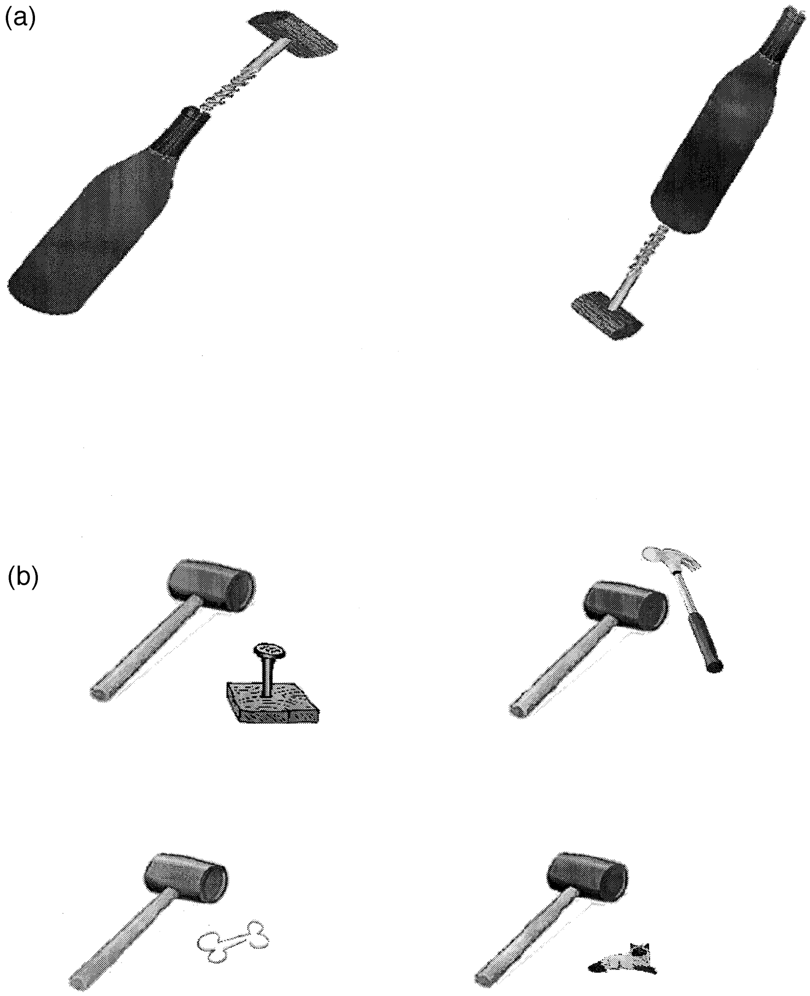

Figure 3. Example stimuli from studies examining the effects of action relations between stimuli on visual extinction (from Riddoch et al., 2003). (a) The stimuli used to contrast report when objects were in correct vs. incorrect positions for action (correct = left, incorrect = right). (b) The stimuli employed to contrast report with objects that are used jointly in action vs. objects that are verbally but not action associated. Hammer and nail are verbal and action associates; hammer and mallet are verbally associated only. The object pairs were matched for verbal association. The objects were re-paired together to form control conditions for the action and verbal association conditions (bottom two pictures).

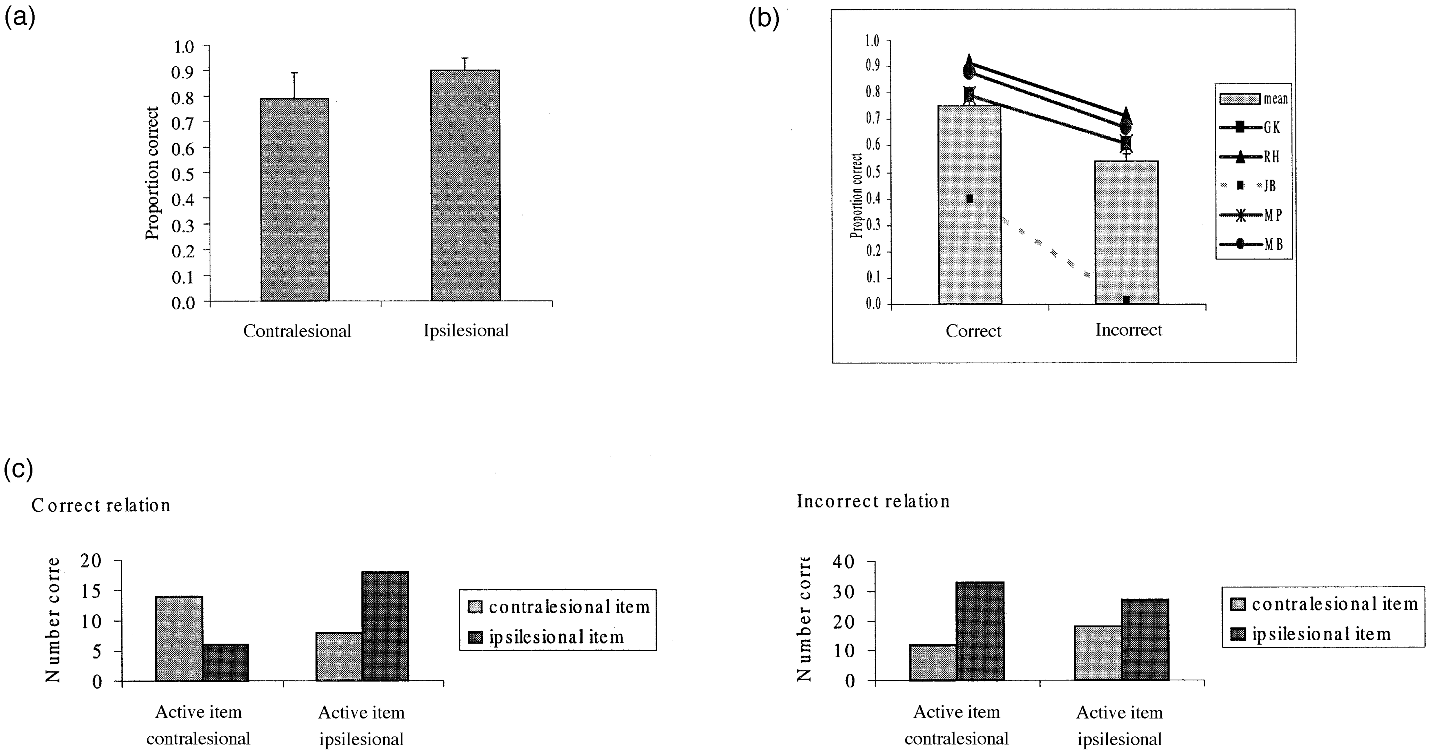

Figure 4. Effects of correct vs. incorrect relations for action on perceptual report. (a) Single item reports. (b) Number of correct reports of two objects. (c) Data from trials on which only one object was reported (on two item trials), as a function of whether the objects were in the correct positions for action and whether the objects were an active or passive member of the pair (after Riddoch et al., 2003).

tended to be identified irrespective of whether it was in the contra- or ipsilesional field. However, in the incorrect location condition, the patients tended to report the ipsilesional item irrespective of whether it was the active or passive partner in the pair (see Figure 4c). This result suggests that having the correct action relations between objects induces a bias in perceptual selection, so that patients attend first to the active partner even when it falls in the contralesional field. This item then tends to be reported even when the ipsilesional (passive partner) is not identified. It follows that the effect of the action relationship here is implicit, affecting performance even when the patient is not aware of the relationship between the objects, since they report only one member of the pair.

In a second study, Riddoch et al. (2003) evaluated whether the improved report on correct location trials was due to varying the visual familiarity of the object pair. Objects in the correct locations are likely to be more visually familiar as a pair than objects in incorrect locations. A familiar pair of objects may be better reported than the same pair in an unfamiliar relationship because the familiar pair actives some form of higher-order recognition unit (e.g., for both objects, as a pair). To test this, the identification of objects that would be used together (an action-related pair) was contrasted with the identification of objects that were associatively related but that would not be used together in an action. Within each pair, one object was designated a target (e.g., a mallet) and it appeared along with either an action-related partner (e.g., a nail) or an associatively related partner (e.g., a hammer) (see Figure 3b). The associatively related partner was chosen by means of the Birkbeck College word association norms. The associative object was given as the first verbal association to the target by over 32% of the sample in the norms. In contrast, the action-related partner was given as the first verbal association to the target by less than 3% of the sample. In addition to this, a group of independent participants was asked to rate the visual familiarity of the objects, as a pair. There was no difference between the action-related pairs and the associatively related pairs in their rated visual familiarity. Three of the original patients (JB, RH, and GK) were tested with both the action- and the associatively related objects, along with unrelated pairs of objects created by exchanging partners for different targets within the action or the association set.[3] All the stimuli appeared on both the contra- and ipsilesional sides, for each patient. There were also single object trials, adjusted so that patients identified about 80–90% of the contralesional objects.

The results are shown in Figure 5. There was little effect of the side the target appeared on, on single object trials (Figure 5a). As expected, there was a drop in

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[3] This meant that the same objects appeared in the action-related experimental condition and its control, and the same objects in the associatively related experimental condition and its control. Note that, because the partners were different in the two experimental conditions, direct comparisons cannot be made.

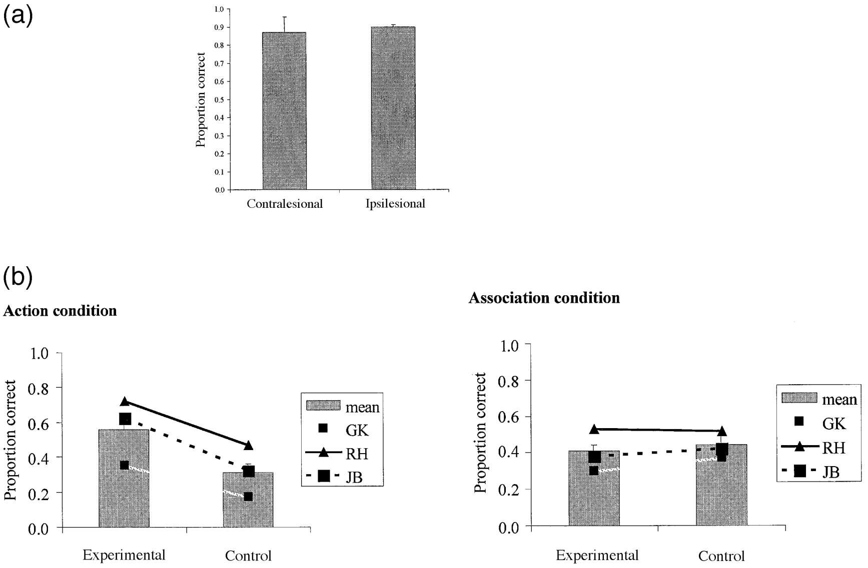

Figure 5. Effects of action vs. verbal association on perceptual report. (a) Single item reports. (b) Number of correct reports of two objects according to whether the objects were action related or associatively related to one another. In these latter cases, performance is measured relative to unrelated baselines created by re-pairing objects from the action- and associatively related conditions (after Riddoch et al., 2003).

performance on two object trials, and the patients showed spatial extinction—errors typically involved the ipsi- but not the contralesional object being identified. Nevertheless more object pairs were correctly identified in the action related condition compared with its control. This contrasts with the associative condition, which did not differ from its control (Figure 5b). Since the object pairs in the action-relation and the association conditions were equally visually familiar, the relative improvement for action-related pairs cannot be attributed to visual familiarity. Also note that, on a guessing account, we would expect the association condition to be favoured—objects in this condition were more likely to be generated as a verbal associate to the target compared with the action condition. Clearly this did not occur. Instead of this we propose that objects placed in correct locations for action are attended as a single pair. Perceptual selection is sensitive to implicit action relations between objects, even when an explicit action is not made to the stimuli.

The study of Riddoch et al. (2003) demonstrates effects of action relations on identifying pairs of objects. However, although the spatial relations between the stimuli are important in bringing about this effect (see Figures 3a and 4b), the data do not show that implicit action relations influence spatial coding—it may be that there is improved report of object identities without explicit recovery of their locations. We have been able to assess whether action affects the recovery of spatial information in one of the patients in the Riddoch et al. study, GK. As indicated above, GK had bilateral parietal damage. Clinically, GK presented with Balint's syndrome (Balint, 1909), characterized by simultanagnosia (appearing to be aware of only one object at a time), and optic ataxia (misreaching to objects under visual guidance) (e.g., see Edwards & Humphreys, 2002, for evidence on GK reaching to multiple objects). Patients with Balint's syndrome can show grossly impaired visual localization, even when motor responses do not have to be directed to objects. For example, GK was unable to discriminate whether stimuli fell above or below fixation even when they were presented 3° into the upper or lower field for up to 1 s (Humphreys, Romani, Olson, Riddoch, & Duncan, 1994). He also made many ''illusory conjunctions'' when reporting stimuli exposed for long durations—for instance reporting a red O and a blue X as a blue O and a red X (Humphreys, Cinel, Wolfe, Olson, & Klempen, 2000; see also Friedman-Hill, Robertson, & Treisman, 1995). This suggests that he had problems in binding stimulus attributes to their locations. In Experiment 2, we exploited this difficulty in recovering and binding location information in order to examine whether binding could be influenced by action relations between stimuli.

EXPERIMENT 2: EFFECTS OF IMPLICIT ACTION RELATION ON SPATIAL BINDING

Method

We used the stimuli from Study 1 in Riddoch et al. (2003), which varied in whether the objects were positioned in the correct or incorrect locations for action. There were nine object pairs, which were positioned in either correct or incorrect locations for action (within each pair). Within one session, the stimuli in the correct and incorrect pairing were presented four times, twice with one object on the left and one on the right and twice with the spatial positions (to the left or right of fixation) being reversed (72 two-object trials). These two-object trials were matched by a set of one-object trials in which each stimulus in the pair was shown alone, in the same spatial location as it appeared on two-object trials (for both the correct and the incorrect pairings; 72 trials in total). The average size of the pictures was 5.5 cm high × 5.9 cm wide. GK took part in four sessions, conducted across consecutive weeks. The stimuli were coloured drawings of objects commonly used in action together, presented for 1500 ms in order to try to optimize GK's ability to identify both the stimuli present on two-object trials. He was asked to identify the objects on each trial, and then to report whether the objects fell to the left or right of his body/fixation. The stimuli were presented using Eprime on a pc. The stimuli were selected from Corel Clip-art

Gallery (www.pstnet.com) and they were presented against a white background. GK saw the stimuli from 50 cm, with the stimuli being preceded by a fixation cross for 3000 ms.

GK (b. 1939) suffered two consecutive strokes in 1986 resulting in damage to the right occipitoparietal cortex, the right temporal-parietal cortex and the left temporal-partietal cortex. Subsequently he has suffered a range of neuropsychological deficits. He manifests Balint's syndrome whose symptoms include optic ataxia (misreaching under visual guidance), simultanagnosia, and extinction. In everyday life, GK has great difficulties in the perception of complex multiple object scenes, and he seems to be aware of one object only (or part of it) at a time. He also has attentional dyslexia (he can report words but not their constitutent letters; Hall, Humphreys, & Cooper, 2001). He is slightly impaired in word finding, but he has intact memory and comprehension. More details on GK's case are reported in Gilchrist et al. (1996) and Humphreys et al. (2000). Testing here was conducted in 2002.

Results

On one-object trials GK identified 140/144 (97%) of the items in his ipsilesional field and 120/144 (83%) of the objects in his contralesional field. Ipsilesional stimuli were reported better than contralesional stimuli, McNemar test of change, $\chi^2(1) = 20.0$. On two-object trials GK identified 81% (118/144) of the objects presented in the correct spatial relations for action and 56% (80/144) of the objects presented in incorrect spatial relations for action. There remained an overall advantage for identifying members of a pair placed in the correct locations for action, McNemar test of change, $\chi^2(1) = 23.3$, $p < .001$, replicating our prior finding (Riddoch et al., 2003). On two-object trials, GK typically missed objects in his contralesional side when the stimuli were placed in the incorrect locations for action (50 out of the 64 errors). When objects were in the correct relations for action he made relatively more errors by reporting the contralesional item (now only 14 of the 26 error trials involved report of the ipsilesional object, $\chi^2(1)= 4.19$, $p < .05$, relative to the incorrect position condition). When the objects were in the correct locations for action, GK tended to report the object that was ''active'' in the action, even when it fell in the contralesional field (on the twelve trials where GK only reported the contralesional item, this item was the active member of pair; see also Riddoch et al., 2003). When the objects were in the incorrect relations for action he tended to identify the ipsilesional item irrespective of whether it was the active member of the pair. When one item was reported GK always reported that this was the only picture present.

The data for GK's localization responses, on trials where he identified both members of a pair, are shown in Figure 6. Even when he could identify both objects, GK was reliably better at reporting the relative locations of the objects

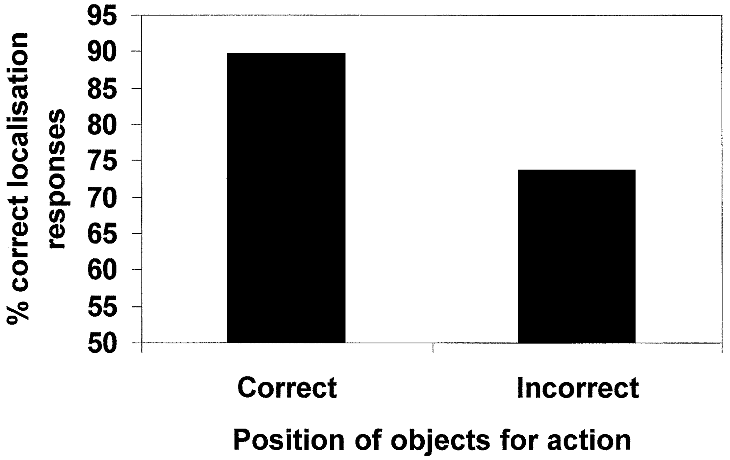

Figure 6. Percentage correct reports by patient GK of the relative spatial locations of objects placed in correct and incorrect positions for action, in Experiment 2. In all cases, GK named both of the objects present. Chance = 50% correct.

when they were in the correct positions for action than when they were in incorrect positions, $\chi^2(1) = 7.76$, $p < .01$ (see Figure 6). Interestingly, on one-object trials where he correctly identified the target, GK only correctly localized 155/261 (59%) of the stimuli. Performance here did not differ from chance ($\chi^2 < 1.0$) and it also fell below the level found on two-object trials even when the stimuli were presented in the incorrect locations for action, $\chi^2(1) = 4.81$, $p < .05$.

Discussion

The basic pattern of data replicate those found by Riddoch et al. (2003). GK showed spatial extinction, generally being better at identifying a single picture in his left field than at identifying the left member of a two-object pair. Despite this, his identification of the stimuli on two-object trials was better when the stimuli were placed in the correct colocations for action compared with when they fell in the incorrect locations. Also, when errors were made on two-object trials he tended to report the active member of the pair, irrespective of its spatial location, when the stimuli fell in the correct locations for action; when the objects were not in the correct locations for action he tended to identify just the ipsilesional stimulus.

We also extended the study of Riddoch et al. (2003) by asking GK to identify the spatial locations of the stimuli he could identify. Here we found two interesting patterns of result. First, though GK was at chance at locating a single object that he could identify, he was relative better at localizing two stimuli, even when the objects were not placed in the correct locations for action. We suggest that this result arose because, when GK could identify the two objects present, he could make a relative location judgement between the objects rather than judging the position of the objects in comparison with fixation or his body position. Given damage to GK's ability to encode spatial information with respect to his body, the relative location judgement should be easier as it can be based on allocentric information between the objects. Second, placing objects in the correct colocations for action influenced his location judgements; location judgements were more accurate when the objects were in the correct colocation for action compared with when they were in the incorrect locations. Action influenced spatial coding.

GENERAL DISCUSSION

We have reviewed and reported neuropsychological data indicating that:

1. Using a tool that reaches into an affected part of space can improve a patient's perceptual awareness of stimuli in that space (Ackroyd et al., 2002).
2. The effect of tool use can come about through visual cueing that is supplemented by motor cueing, helping a patient attend to a neglected region of space (see Experiment 1); this effect of visuomotor cueing can operate in addition to any effects caused by ''near'' space being remapped to encompass a more distal area around the tool (cf. Maravita et al., 2002).
3. Even when an explicit action is not made to an object, implicit action relations between objects can influence spatial attention. This reduces the effects of spatial extinction on the perceptual identification of objects in the correct spatial relations for action (Riddoch et al., 2003). These effects of placing objects in the correct colocations for action can influence performance even when only one member of a pair can be identified—hence action-relations appear to be coded unconsciously.
4. Placing objects in the correct co-locations for action can also influence how well the objects are bound to their spatial positions; for a patient with Balint's syndrome there were fewer mislocalizations of stimuli placed in the correct locations for action than stimuli placed in incorrect locations (see Experiment 2).

These results are consistent with the idea that perception and action are interactive rather than independent processes. If this were not the case, then it is difficult to understand how motor cueing enhances any effect of visual cueing, to reduce neglect in object detection tasks.

Moreover, interactions between action and perceptual selection are dependent not only on actions being made to objects but also on the action relations present between stimuli (i.e., whether stimuli are in appropriate relative locations to be used together). These effects of action relation occur over and above any effects due to associative or visual familiarity (Riddoch et al., 2003). Thus the effects seem not to come about solely by associative learning of individual object pairings.

To account for the data on extinction, we suggest that perceptual selection is sensitive to the potential for action between known objects in the environment. This ‘‘potential for action’’ itself may depend on factors like the positions of the objects with respect to the observer (including the distance from an effector; see Tipper, Howard, & Houghton, 1998; Tipper, Howard, & Jackson, 1997), their orientation (Humphreys & Riddoch, 2001), and the task goals (Riddoch, Edwards, Humphreys, West, & Heafield, 1998). The action-relation factors that determine selection may involve learned associations with specific objects, but also associations between actions and parts that generalize across different objects (e.g., handles of different cups, dials of different instruments). In each case, we suggest that our attentional systems strongly ‘‘weight’’ objects based on these associations with action. Moreover, we propose that we learn to select two or more objects together if their cooccurrence is correlated with the objects being used in a joint action. Given that we find that action-relations are a stronger trigger for attention than associative relations between objects (Riddoch et al., 2003), we maintain that cooccurrences based on action are more important for learning and attention than ‘‘mere’’ (associative) cooccurrence alone. This is perhaps not surprising, given that any change in the environment contingent on an action provides new statistical information that the objects are indeed linked.

The results on spatial localization indicate that, in addition to effects on selection for perceptual report, action relations can facilitate the binding of objects to space. In a patient such as GK, with Balint’s syndrome, it is possible that the improvement in spatial binding comes about because, in the correct relations condition, objects are attended together. Coding the relative locations of stimuli may be relatively difficult if the stimuli are attended in a serial fashion, leading to mislocalizations even when both items are identified. Alternatively, the action relation between the stimuli may provide extra spatial information (e.g., coded in terms of an implicit motor code) that directly facilitates binding. Further work is needed to evaluate these different proposals.

The neural substrates of action coding

As well as informing us about the functional influence of action on perception, the neuropsychological data we have presented provide some information on the neural substrates of action coding. Perhaps the most popular view, when discussing the relations between perception and action, is that ‘‘vision for action’’ is controlled by regions of dorsal visual cortex (e.g., Milner & Goodale, 1995). Research on brain imaging is consistent with this. For example, the parietal cortex has been shown to be active when actions are observed with an intention to imitate or memorize for future recognition (Decety et al., 1994, 1997; Grèzes, Costes, & Decety, 1998), and when reaching and grasping responses are observed relative to a nonprehensile gesture to an object (Passingham, Toni, Schluter, & Rushworth, 1998). From this, we might expect that effects of both explicit action (reaching to objects, or providing motor cues to attention) and implicit action (having objects in the correct colocations for action) would depend on a dorsal visual route. The difficulty with this view is that we might expect damage to the parietal lobe to disrupt the ability of a patient to show modulatory effects of action on perception. As we have demonstrated, this is not the case. In all of the patients reviewed above, there was damage to the parietal lobe, and yet there were effects of both explicit action cueing and implicit action relations between objects.

An alternative view is that effects of action relations between stimuli, and of action on perception, operate through undamaged (e.g., more ventral) areas of cortex in these patients. At least one imaging study indicates that processing through more ventral visual areas is sensitive to action affordances from objects. Phillips, Humphreys, Nopenney, and Price (2002) had participants make action or ''image size'' decisions to pictures of objects, nonobjects, and words. Relative to the ''image size'' baseline, the action tasks activated the left inferior frontal, the left posterior middle temporal, and the left anterior temporal cortices. The activation was generally greater and more widespread when words were presented as stimuli relative to objects and nonobjects, presumably because the retrieval of learned actions from words is more difficult, and requires more semantic processing, than the retrieval of action from objects (see Chainay & Humphreys, 2002, for evidence with normal observers). However, for nonobjects relative to words there was some increased activation in the left occipitotemporal cortex and the anterior medial fusiform gyrus, for action decisions relative to ''image size'' decisions. These latter regions have been linked to visual processing of object-like perceptual structures (e.g., Malach, Reppas, Benson, Kwong, Jiang, & Kennedy, 1995). This in turn suggests that action decisions involve detailed processing of object structure, and perhaps direct association of actions with those structures, lessening the demand for semantic retrieval. These ventral areas might subserve the action effects we have observed in patients with parietal lesions. Alternatively it may be that patients remain able to respond on the basis of partial activation within a damaged parietal system sensitive to action relations between stimuli and to actions made to stimulus locations. The more general point is that the action effects we have studied could be contingent on neural structures other than the regions of dorsal cortex involved in the online visual control of action (cf. Milner & Goodale, 1995), and could include ''downstream'' influences in ventral cortex from visuomotor cueing (see Schneider, 1995, for discussion of this) and ventral activation based on action-related associations between stimuli in the environment. The precise neural areas subserving these effects might be addressed in future through appropriate functional imaging studies with the patients. The interactive nature of perception and action, however, suggests that a strict distinction between ''dorsal'' action and ''ventral'' perceptual processes may not operate in many aspects of visuomotor performance.

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