# Seeing the action: neuropsychological evidence for action-based effects on object selection

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**Previous studies have shown that selection for perceptual report is often limited to one object at a time, with elements being selected together if they belong to part of the same perceptual group. Here we used the neuropsychological phenomenon of extinction in human patients with parietal lesions to show that selection is influenced also by action relations between objects. Performance was better for objects that were positioned spatially so that they could be used together, relative to objects that were positioned inappropriately for their combined use. The action relation was critical, as performance for pictures did not improve if the items were only verbally associated. We found the opposite result with words. Effects of action relations emerged even on trials where only one object could be reported, showing implicit coding of 'action' units for selection. The effects of verbal associations may instead reflect priming between lexical entries.**



The neuropsychological phenomenon of extinction occurs when two stimuli are simultaneously presented (one to each hemifield), and the patient—who has no difficulty seeing each stimulus presented alone—reports seeing only one of them[1]. Although classically associated with parietal damage[2], extinction can result from a variety of brain lesions[3]. This deficit in perceptual report when multiple stimuli compete for selection can be attributed to a chronic limitation in visual attention resulting from the brain lesion[4].

The constraint on visual selection in patients with extinction can be overcome by grouping stimuli into single objects. Several grouping factors have been shown to be important, including collinearity[5,6], connectedness[7,8], common shape[5,8], common contrast polarity[5,8], common region[8] and whether elements are parts of a known shape[9,10]. In one study, a patient could select two words if they formed a verbal association, but when unrelated word pairs were presented, selection was limited to one word[11]. Here, we confirmed this effect with words, for at least some patients showing extinction. We attribute this to priming between associated lexical entries. For objects, in contrast, we found that action relations rather than verbal associations influenced visual selection. Uniquely for objects, effects of action relations emerged even on trials when only one of the two stimuli could be identified, with the action relation biasing identification of the salient member of the action pair. Thus we conclude that implicit coding of the action relationship modulates visual selection. Our results have implications not only for theories of visual selection, but also for theories of object and word processing and for understanding the nature of the representations accessed by these stimuli.

In experiment 1, we contrasted performance (reporting) for objects that were placed in the correct relative positions for action with performance for objects that were not (**Fig. 1a**). Five patients were tested (JB, MB, RH, GK and MP; see **Fig. 2** for scan details). Three patients had right parietal lesions (JB, MB and MP), one had a left parietal lesion (RH) and one had bilateral parietal lesions with left-side spatial extinction (GK)[5,8]. Either a single picture was presented to the left or right of fixation, or pairs of pictures were presented with one to either side of fixation. Stimulus pairs were selected if they could be used together in action (for example, corkscrew and wine bottle; **Table 1**). On two-item trials, the pictures were presented either in the correct positions for action (the corkscrew going into the cork at the top of a wine bottle) or in the incorrect positions for action (the corkscrew going into the bottom of the wine bottle). On single-item trials, the individual objects were placed in the same locations as were used for both the correct position and incorrect position trials (when two items were present). The task was to identify the objects on each trial (or to indicate whether an object was present, even if it could not be identified).

Experiment 2 was similar to experiment 1, except that a further condition was added to compare performance when objects were in appropriate action relations to that when they were associatively related. We used the same target objects in both critical conditions, pairing them with different partner objects to create the action-related and the associative-related conditions (Methods; **Fig. 1b**). For the associative condition, the item paired with the target always corresponded to the name generated most frequently in response to the target, according to the Birkbeck Word Association Norms[12]. In the action-related condition, the item paired with the target was generated much less frequently as a verbal associate (**Table 2**). The action-related and associated picture pairs were matched for visual familiarity (Methods). Objects in the action condition were always in the correct relative locations for the action.


**Fig. 1.** Example stimuli for experiments 1 and 2. (**a**) Example stimuli used in Experiment 1 in the correct (left) and incorrect (right) positions for action. (**b**) Example action (left) and associatively related (right) pictures used in Experiment 2.

To control for the effects of the different partner objects used in the critical pairings, we also had two-item control trials in which we re-paired items within the action-related and associative conditions. Experiment 3 replicated experiment 2, except that words, rather than pictures of objects, were presented. Owing to subject availability, only three of the original patients (JB, RH and GK) took part in experiments 2 and 3. Overall, we found that performance was better when objects were positioned spatially so that they could be used together (relative to when they were positioned incorrectly for action). The action relation seemed to be critical, as performance for pictures did not improve if the items were verbally associated. The opposite result occurred with words.

## Results

The results for experiment 1 are shown in **Fig. 3**. Performance on single-item trials was generally better overall than performance on two-item trials, confirming that the patients were subject to visual extinction. Of critical importance was how identification varied between the main two-item conditions. To analyze this, the number of 'two-item correct' trials were entered into a mixed-design ANOVA, with condition (correct versus incorrect position) treated as a within-subjects factor and patient as a between-subjects factor. Each session was entered as a subject nested within the patient factor. There was a main effect of condition ($F_{(1,5)} = 238.08$, $P < 0.0001$), indicating better report of two items when they appeared in the correct relations for action relative to when they did not. This did not interact with the Patient factor, indicating that it generalized across patients ($F_{(4,5)} = 2.48$, $P = 0.173$).

With the object pairs in experiment 1, one object was typically used to effect an action and the other was acted upon (for the corkscrew and bottle pair, the corkscrew is the 'active partner' and the bottle the 'passive partner'). There was no effect of

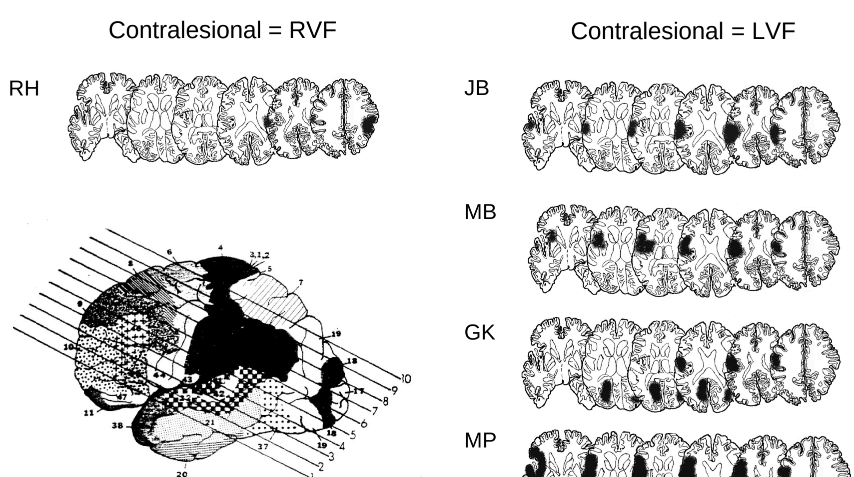



**Fig. 2.** Lesion reconstructions in the patients from MRI scans. Lesions have been re-drawn onto standard slices. Bottom left, the ten slices used. Only slices 3–8 are shown here. The left half of each slice represents the right hemisphere. For RH, the contralesional stimulus fell in his right visual field. For the other patients, the contralesional stimulus fell in the left visual field[19].

**Table 1. Picture stimuli used in experiment 1 (view stimuli in Supplementary Fig. 1 online).**

| | Active partner | Passive partner |
|---|---|---|
| | corkscrew | bottle |
| | golf club | golf ball |
| | toothpaste | tooth brush |
| | watering can | flowers |
| | comb | hair |
| | bottle | glass |
| | screwdriver | screw |
| | spanner/wrench | nut |
| Average surface area (range) | 33.4 cm$^2$ (12–90) | 48.1 cm$^2$ (6–144) |

the relative positions of the active and passive partners on two-item correct reports ($F_{(1,5)} < 1.0$), and no interaction with patient ($F_{(4,5)} = 1.50$, $P = 0.32$). There were 65.6% correct two-item responses when the active partner was on the ipsilesional side and 70% when it was on the contralesional side.

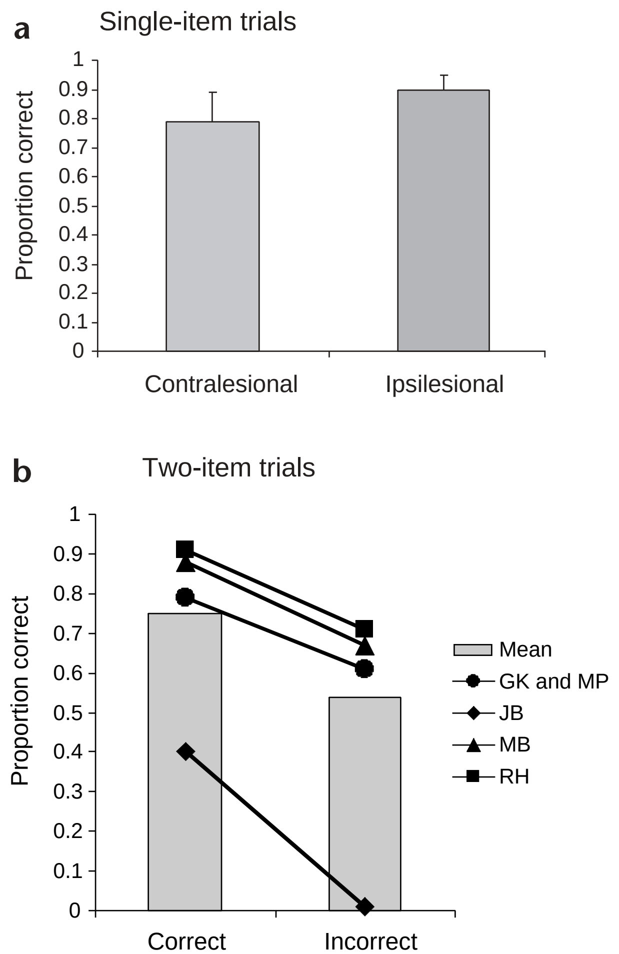
We also examined whether the action relation between stimuli on two-item trials had an effect, even when only one item was identified correctly. We contrasted the numbers of trials in which there was correct report of either the ipsi- or the contralesional stimulus. These data were submitted to a log linear analysis with three factors: condition (correct versus incorrect position for action), side of active partner (active partner on the contralesional versus the ipsilesional side) and position of item reported (contra- versus ipsilesional item). The best-fitting model was based on a three-way interaction between condition, side of active partner and position of item reported ($\chi^2_{(1)} = 8.70$, $P < 0.01$). Performance was then analyzed separately as a function of whether objects were in the correct or incorrect spatial relations with respect to one another. When objects were in their correct spatial relations for action, there was an interaction between side of active partner and position of item reported ($\chi^2_{(1)} = 7.15$, $P < 0.01$), resulting from better reports of the active object, irrespective of whether the active partner fell in the ipsi- or contralesional field. In contrast, when the objects were not in the correct positions for action, there was only a main effect of position ($\chi^2_{(1)} = 10.19$, $P < 0.01$). That is, we found better reporting of the ipsilesional than contralesional object, irrespective of which was the active partner in the pair (**Fig. 3c**).

Overall, the results from experiment 1 show that the patients were more likely to select two items on a trial if the items were positioned in the correct relative locations for action both when the 'active partner' in a pair appeared on the contralesional side and when it appeared on the ipsilesional side. Furthermore, having the correct spatial relations for action affected performance, even when only one item was identified correctly; there was a bias to report the 'active partner' in a pair, irrespective of whether this object was in the ipsi- or contralesional field. This suggests an effect of implic-

**Table 2. Picture stimuli used in experiments 2 and 3 (view stimuli in Supplementary Fig. 2 online).**

| | Target | Action-related action item | Control item | Associatively related associate | Control item |
|---|---|---|---|---|---|
| | cauldron | ladle | bow | witch | violin |
| | cello | bow | ladle | violin | witch |
| | dog | bone | tin opener | cat 1 | can |
| | peach | knife | bowl | plum | fork |
| | tin | tin opener | nail | can | hammer |
| | noodles | chopsticks | ruler | a Japanese | pen |
| | spoon | bowl | cheese | fork | cat 1 |
| | pencil | ruler | chopsticks | pen | a Japanese |
| | mouse | cheese | knife | cat 2 | plum |
| | mallet | nail | bone | hammer | cat 2 |
| Average association rating with target[1] | | 1.9% (s.d. 2.0%) based on 6/10 items | | 32.3% (s.d. 13.7%) | |
| Average surface area for pictures: experiment 2 | 31.3 cm$^2$ (range 8.2–45.7) | 11.9 cm$^2$ (range 2.3–19.1) | | 14.8 cm$^2$ (range 5.5–26.5) | |
| Average width of pictures: experiment 2 | 6.1 cm (range 1–9) | 6.2 cm (range 3–11) | | 3.9 cm (range 1–6) | |
| Average length of words: experiment 3 | 5.5 cm (range 5–8) | 5.6 (range 3–10) | | 4.5 cm (range 3–8) | |
| Mean ratings of visual familiarity to the target using a 5-point scale (by 9 independent participants)[2] | | 4.2 | 1.4 | 4.0 | 1.3 |

[1] Based on the Birkbeck Word Association Norms[15]
[2] Analyzed across items, there was an effect of whether the stimuli were in an experimental or control pair ($F_{(1,9)} = 98.89$, $P < 0.001$), but there was no difference between the associates and the action items ($F < 1.0$) and no interaction between item-type (associate, action) and relatedness (experimental versus control; $F_{(1,9)} = 1.04$, $P > 0.05$).



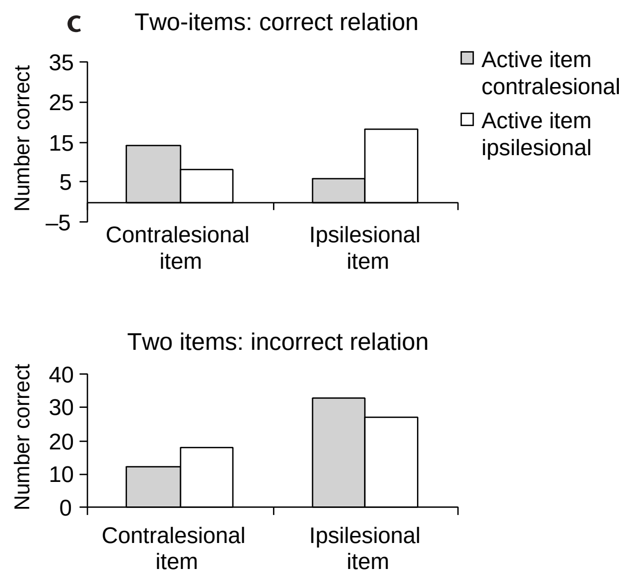




**Fig. 3.** Experiment 1. (**a**) Identification performance for single pictures presented in the ipsi- and contralesional fields, in the correct and incorrect action relation conditions. (**b**) Identification performance for both pictures on two-item trials. (**c**) Item reported on error trials when two items were present as a function of the position of the active partner in both correct (top) and incorrect (bottom) action-relation conditions.

it coding of action relations between the objects. However, when the objects were in incorrect positions for action, there was better report of the ipsi- over the contralesional stimulus, irrespective of whether the active partner was on the contra- or ipsilesional side.

The results for experiments 2 and 3 are given in **Figs. 4–6**. In experiment 2 (with pictures), identification was again better on single- versus two-item trials. Performance on two-item trials was assessed by comparing the number of fully correct two-item reports in the critical experimental conditions (using action- and associatively related stimuli) with identification of the same stimuli in the baselines. There were two within-subjects factors: condition (action- versus associatively related) and relatedness (experimental versus control); patient was treated as a between-subjects factor, with test session entered as the subject factor. There was a main effect of relatedness ($F_{(1,6)} = 8.69$, $P = 0.026$) and a significant interaction between condition and relatedness ($F_{(1,6)} = 9.39$, $P < 0.025$). There was no effect of patient and no interaction involving this factor. For the action-related objects, there was a reliable difference between the experimental and control conditions ($F_{(1,6)} = 16.93$, $P = 0.006$), which was not qualified by an interaction with patient ($F < 1.0$). For the associatively related objects, there was no difference between the experimental and control conditions ($F < 1.0$), which again was not qualified by an interaction with patient ($F < 1.0$). For the action-related stimuli alone, target identification in the experimental (related) condition was better than that in the (unrelated) control.

For experiment 1, we also analyzed incorrect trials in the two-item condition. Here we assessed the report of the critical target item (appearing in each condition) in the contralesional field, when it was the only one of the two items reported (**Fig. 5a**). In the action experimental condition, the contralesional target was reported more often than in the action control ($\chi^2_{(1)} = 11.35$, $P < 0.01$). In contrast, the comparison between the experimental and control condition for associatively related objects revealed no difference in the proportions of error trials where the contralesional target was identified ($\chi^2 < 1.0$).

These data confirm those from experiment 1 and show that extinction is reduced for objects that appear in the correct relative spatial locations for action. There was no benefit for objects that were associatively related to one another, even though the action- and the associatively related stimuli were rated as equally visually familiar as object pairs (Methods). Hence there appears to be an effect of the action relation over and above effects of associative relation and of visual familiarity between pairs of objects. We also confirmed effects of the action relation between objects, even when only one member of a pair was reported (the action relation boosts identification of the contralesional object).

The data for experiment 3 are given in **Figs. 5** and **6**. As for the earlier experiments, report was better on single than on two-item trials. The two-item trials were analyzed in the same way as for experiment 2. There was a main effect of relatedness ($F_{(1,6)} = 16.16$, $P < 0.001$), an interaction between relatedness and patient ($F_{(2,6)} = 5.32$, $P < 0.05$) and an interaction between relatedness, condition and patient ($F_{(1,6)} = 4.34$, $P < 0.08$). There was an advantage for the experimental over the control condition when the words were associatively related ($F_{(1,6)} = 18.29$, $P = 0.005$), but this tended to vary across patients ($F_{(1,6)} = 4.09$, $P = 0.076$ for the interaction between relatedness and patient). When the words were action-related, there was no effect of relatedness ($F < 1.0$). JB and RH showed an advantage for the exper-

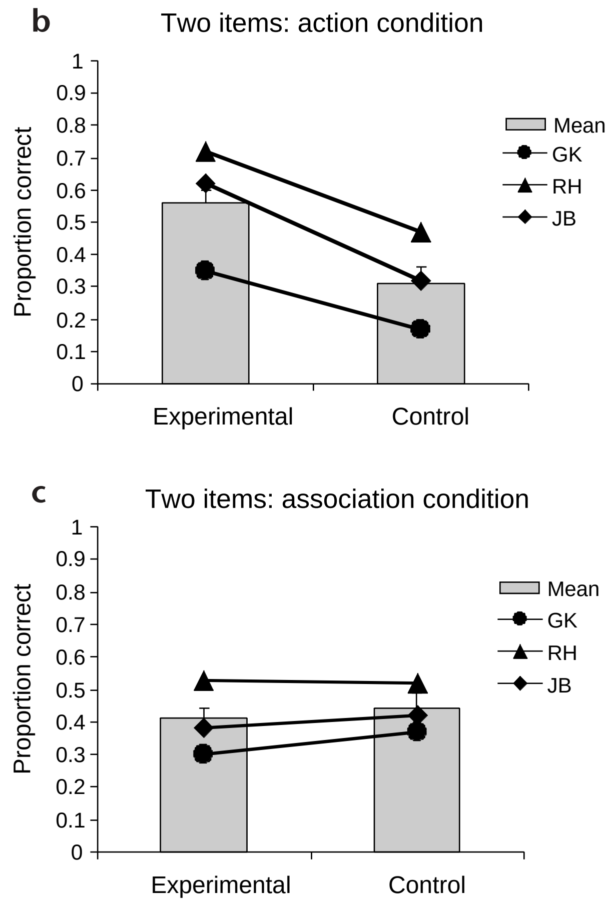




**Fig. 4.** Experiment 2. (**a**) Identification performance for single pictures presented in the ipsi- and contralesional fields. (**b**, **c**) Identification performance for both pictures on two-item trials in experiment 2.

imental relative to the control condition, but only for the associatively-related stimuli. GK did not show a strong advantage for either associatively or action-related stimuli, compared with the unrelated baselines (Methods).

We again analyzed the data on error trials when two items were present (**Fig. 6b**). There was no difference in the proportions of errors that involved correct report of the contralesional target in the experimental and control conditions, for either the action-related items (experimental versus control, $\chi^2 < 1.0$) or the associatively-related items ($\chi^2_{(1)} = 1.19$, $P > 0.05$). That the contextual relationship did not affect report on two-item error trials suggests that the contextual effects occurred in different ways for words (experiment 3) and pictures (experiments 1 and 2). With pictures, there were implicit effects of the action relation between the stimuli on selection of the item for report, even when only one object was identified. With words, there were no such implicit effects; this suggests that effects on reporting both items present may have arisen through priming from one of the identified items (usually the ipsilesional stimulus). Priming occurred between associatively related words but not between words corresponding to objects that would be used together in action.

## Discussion

Our results indicate that extinction between separate perceptual objects can be reduced if the objects are placed in the appropriate relative positions for action. The benefit for correctly positioned, action-related objects was evident for all patients, in both experiment 1 (relative to the same items positioned incorrectly) and experiment 2 (relative to the same items but in incorrect pairs). The reduction in extinction was not due simply to objects appearing in familiar pairs. The objects comprising the action-related and associatively related pairs in experiment 2 were rated as equally familiar as pairs. Furthermore, related stimuli (experimental conditions) were rated as more familiar than unrelated stimuli (control conditions), yet only objects in the action-relation condition were identified better than in the control. For successful reporting of both objects, they had to be presented in appropriate relative positions for action.

Several explanations for these results can be ruled out from our data: guessing or attentional cueing from the ipsilesional item[13], effects on attentional disengagement from the ipsilesional item in the related conditions, and priming of the identification of the contralesional item from the ipsilesional stimulus[14]. If guessing from the ipsilesional item were important, then the spatial relations between the stimuli would not matter; experiment 1 showed that they do. Furthermore, there were no incorrect false-alarm responses on single-item trials in the action-related condition. Such errors would occur if guessing from ipsilesional stimuli contributed to performance in the experimental condition on two-item trials. Some patients reported being aware of a second stimulus (which they failed to identify), but this was not so for patients MP and GK. These patients typically reported that only one item was present under extinction conditions, yet they produced effects of at least equal magnitude to the other patients. Finally, we would not expect guessing to be sensitive to the contrast between action- and associative relations. Indeed, the action-related stimuli in experiment 2 were less likely to be generated than the associatively-related stimuli as a word associate to the targets (Methods). Guessing would, in fact, favor the associatively related stimuli.

We may also rule out the following explanations: (i) attentional cueing from the ipsilesional item[13], (ii) a related contralesional item facilitating attentional disengagement from the ipsilesional item and (iii) priming of the identification of the contralesional item from the ipsilesional item. We found no effect of the relative positions of the active and passive partners on two-item reports. The disengagement account is also contradicted by the fact that action relations could be influential even when only one of the two items on a trial was identified. In experiment 1, the presence of objects in the correct

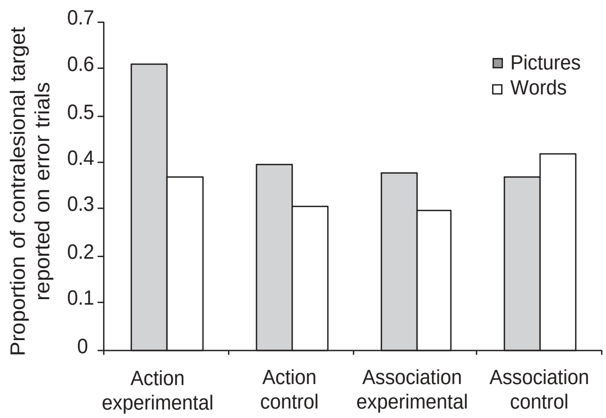



**Fig. 5.** Percentage of correct responses to contralesional targets on error trials in the two-item conditions of experiments 2 and 3, as a function of experimental condition. Gray bars, data from experiment 2 (pictures); white bars, data from experiment 3 (words).

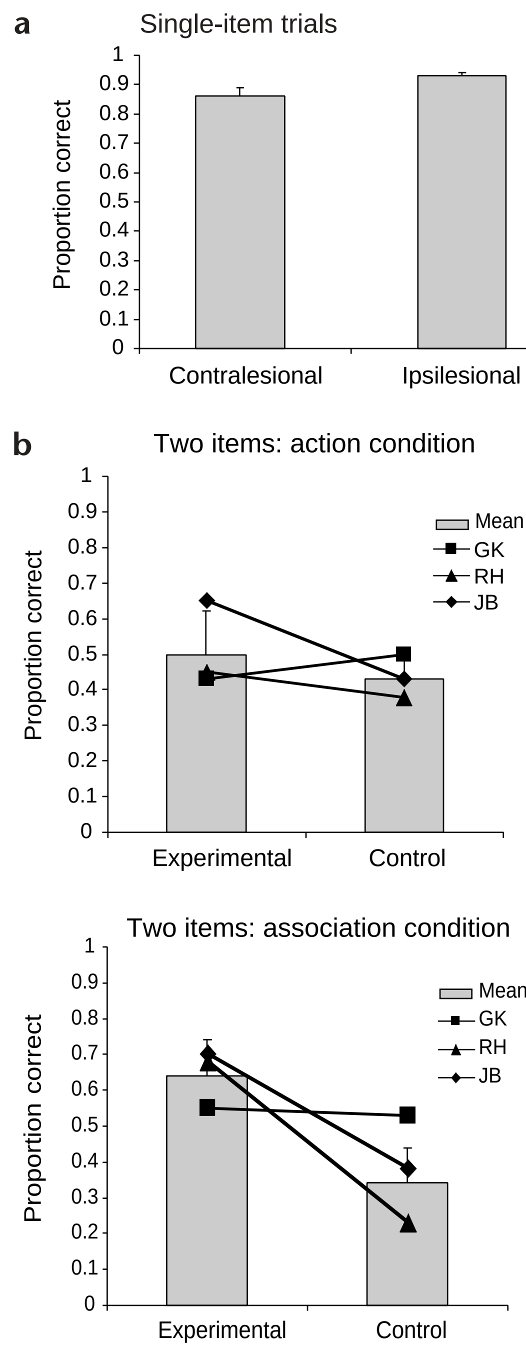



**Fig. 6.** Experiment 3. (**a**) Proportion correct on single-item trials. (**b**) Proportion correct on two-item trials for the action condition (top) and association condition (bottom).

spatial positions for action-biased selection to the active partner within an action pair (whether ipsi- or contralesional). Experiment 2 showed the same effects, but only for target objects in the correct action relations. On two-item trials where only the contralesional target was identified, the bias to this item could not have resulted from improved disengagement from the ipsilesional stimulus (which would have been identified, having engaged attention first). These error data similarly rule out an account in terms of priming from the ipsilesional stimulus, which may facilitate identification of the contralesional item[14]. Priming predicts that there should be no effect of the action relations between items on trials where participants only identify one of the two objects present. Instead, the results indicate that action relations between objects can influence performance implicitly, even when the action relations cannot be explicitly recovered (and only one of the two stimuli present is reported). Action relations between the stimuli implicitly biased visual selection.

The results with objects stood in contrast to those with words. When words were presented, there was a benefit for associatively related stimuli but not for words corresponding to action-related objects (at least for two of the three patients in experiment 3). This benefit is unlikely to be due to guessing. Guessing should not generate better report of associatively related words but not of associatively related objects. Also, as before, there were no incorrect guesses of associatively related stimuli on single-item trials. With words, however, we found no evidence for implicit effects on trials where only one item was reported. It is possible that priming from the ipsilesional item contributed to good conjoint report of the contralesional, associatively related word. Consistent with this, the effects were most apparent for two patients (RH and JB), who reported some perceptual information about the extinguished stimulus. Priming could have helped the patients recover the identity of the word from the degraded perceptual input.

From these data, we suggest that different relationships between objects and words influence visual selection. For objects, action relations are more important; for words, associative relations are more important. Current theories account for recovery of extinction between parts of a simple object by suggesting that activation of a stored representation helps to 'glue the parts together' for visual selection[4]. The present results for objects can be accommodated by an extension of this account if we hold that context-sensitive representations can span several stimuli. Activation of such representations provides the 'glue' for the two objects present on a trial to be selected together. When each item then has to be identified, the action relationship between stimuli can also implicitly bias the identification process, favoring the object within the pair that would be active in the action (as we found on error trials in the two-item condition, with action-related objects). For objects, the representations that 'glue' the stimuli together are sensitive to action rather than to associative relations between stimuli. For two objects to cohere as a single unit for selection, then, it seems that associative co-occurrence is not sufficient. This may be because our learning of visual units is contingent on an event-related parsing of the world, itself determined by causal action between objects. Action relations may provide a more stable part of the learning environment than mere associative co-occurrence.

In contrast, associative relations between words may be important for word identification, where co-occurrence determines the meaning of sentences. Associative links between lexical entries for words may facilitate word recognition when perceptual input is impoverished. From the different results for pictures and words we conclude that contextual knowledge, sensitive to action between objects, is independent of lexical knowledge about word associations. The distinction between action-related and lexical knowledge fits with the notion that our concepts of objects are based on a distributed representation in which different forms of stored information can gain privileged activation from different stimuli—objects gain privileged access to action knowledge, words to lexical knowledge[15,16]. Our findings also indicate that access to action-related knowledge in particular can still take place despite parietal damage.

## Methods

**Participants.** JB, a left-handed housewife born in 1935, suffered a stroke in 1999. The magnetic resonance imaging (MRI) scan showed damage to inferior parietal and frontal areas of her right hemisphere, including the angular and supra-marginal gyri, the post-central gyrus and the inferior frontal gyrus. There was also evidence of an earlier infarct affecting the left occipital lobe. She had left-side neglect in reading and writing and showed left-side extinction on double simultaneous stimulation.

MB, a right-handed housewife born in 1942, suffered a stroke in 1995 that affected several regions within her right hemisphere: the inferior frontal and superior temporal gyri (minimally), the inferior parietal lobule (affecting the supramarginal gyrus but sparing the angular gyrus) and the ventral putamen. Neglect was not apparent on standardized clinical tests, but could be seen on brief visual presentations[17].

RH, a left-handed plumber born in October 1933, suffered a left-hemisphere stroke in 1999. The lesion affected the left inferior parietal and superior temporal lobes, including the angular gyrus. He did not show neglect on many standard tasks requiring spatial scanning, but did show object-based neglect when reading single words and identifying chimeric objects (errors on the right side of the stimuli). He also showed right-side extinction on double simultaneous stimulation.

GK, a right-handed business man born in 1939, suffered two consecutive strokes in 1986. These produced bilateral lesions affecting the right medial occipital parietal region (including the cuneus and precuneus), the right temporo-parietal region and the left temporo-parietal region. GK has Bálint's syndrome (optic ataxia, simultanagnosia and impaired voluntary eye movements) and left-side neglect. He shows left-side extinction with bilateral stimulus presentations[5,8].

MP, a left-handed former tool worker born in 1947, suffered an aneurysm of the right middle cerebral artery in 1992, resulting in cerebral artery occlusion and infarct resulting in damage to frontotemporal parietal regions of his right hemisphere, including the inferior frontal gyrus, the superior temporal gyrus, the supramarginal and angular gyri and the post-central gyrus. MP exhibited unilateral left neglect on the standardized clinical tests[18].

Informed, written consent was obtained from all participants.

**Experiments.** The experiments were run on a PC using E-prime software. In experiment 1, nine pairs of objects typically used together were selected from the Corel Clip-art Gallery (www.pstnet.com). Stimuli were realistically colored and presented against a white background. Within each pair, one item was depicted as the active partner; the other item (passive partner) was the recipient of the action. The stimuli are listed in **Table 1**.

Item pairs were presented in two different ways: one preserving the correct action relation (the corkscrew about to be inserted into the cork of the bottle), and the other presenting an incorrect action relation (the corkscrew about to be inserted into the base of the bottle) (**Fig. 1a**). In both the correct and the incorrect pairings, the stimuli were presented four times in a block: twice with object A on the left and object B on the right, and twice with the left-right positions reversed. This created 72 two-item trials (9 pairs × 2 left-right positions × 2 correct-incorrect relative positions × 2 repeats). On single-item trials, the individual objects were presented in the same spatial locations as in the double-item trials ($n = 36$ left-side and $n = 36$ right-side single stimuli). In total, there were 144 trials, which were presented in two sessions (72 randomized trials per session; left, right and double trials equally distributed across sessions). On two-item trials, the stimuli used in block 1 were repeated in block 2. On single-item trials, stimuli appearing on the left in one block were presented on the right in the second block, and vice-versa. With double displays, the point of contact between the two items was at fixation. Exposure durations differed across patients with the aim of achieving approximately 85% correct identifications of single items on the contralesional side (16 ms for JB, 32 ms for MB, 200 ms for RH, 500 ms for GK and 200 ms for MP). Patients were run individually in a semi sound-proofed room. Before the first session, the 18 different stimulus items (that would form the nine pairs) were presented individually under unlimited exposure conditions to ensure correct identification. For the experimental procedure, patients were seated approximately 50 cm in front of a VDU and asked to identify the items which could be presented singly or in pairs near the center of the monitor. They were also asked to report whether they were aware of the presence of a stimulus even if they could not identify it. Each trial was preceded by a fixation cross for 3,000 ms. Trials were self-paced.

A similar methodology was used in experiments 2 and 3. For experiment 2, ten new target pictures were selected, and each was paired with either an associatively related partner or an action-related partner (**Table 2**). Control conditions were created specifically for each experimental condition by re-pairing the items within each experimental set (pairing each target with a partner that would create either an associative or a functional relationship with a different target). This ensured that the same stimuli appeared in the experimental and control conditions (though the partners differed for the action- and associatively-related stimuli). Analyzed across items, there was an effect of whether the stimuli were in an experimental or control pair ($F_{(1,9)} = 98.89$, $P < 0.001$), but no difference between the associates and the action items ($F < 1.0$) and no interaction between item-type (associate, action) and relatedness (experimental versus control, $F_{(1,9)} = 1.04$, $P > 0.05$). On all two-item trials, the target item could appear on both the left and right sides of fixation (with the partner appearing on the opposite side). This meant that there was a total of 80 two-item trials (20 per condition; 10 pairs × 2 positions per pair). In the single-item conditions, the stimuli were presented in the same spatial location that they had occupied when part of a stimulus pair. There were 100 single-item trials, 50 each where the stimulus was presented to the left and right of fixation (for example, 10 target items, 10 trials for the action-related partner, 10 trials for the action control, 10 trials for associate-related partner, 10 trials for the associate control). Each subject took part in three separate sessions, each consisting of 180 trials. As in experiment 1, the exposure duration varied across the different subjects (GK, 2,500 ms; JB, 200 ms; RH, 30 ms). Experiment 3 was the same as experiment 2 except that words rather than pictures were used as stimuli. The words corresponded to the names of the items used in experiment 2. Words were presented in lower case (black, bold Arial font; **Table 2**). RH and GK completed experiments in the order 1,2,3; JB completed experiments in the order 2,3,1.

*Note: Supplementary information is available on the Nature Neuroscience website.*

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**Competing interests statement**

*The authors declare that they have no competing financial interests.*

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