

Priming of Color and Position during Visual Search in Unilateral Spatial Neglect

Árni Kristjánsson¹, Patrik Vuilleumier², Paresh Malhotra³,
Masud Husain³, and Jon Driver¹

Abstract

■ We examined priming of visual search by repeated target location or color in two patients with left visual neglect and extinction, following strokes centered on the right inferior parietal lobe. Both patients, like the healthy controls we tested, showed intact priming, with performance speeded when either the location or color of a singleton target was repeated over successive trials in a standard search condition (Experiment 1). This was observed both *from* and *to* targets on the contralesional (left) side. Moreover, priming of search was still observed even when a return of fixation back to display-center was required between successive trials (Experiment 2). When

briefly displays were used (Experiment 3), the patients often failed to detect left targets. This situation revealed an important dissociation: Whereas location priming only arose from preceding left targets that had been consciously detected, color priming (possibly arising within the intact ventral stream) did *not* depend on awareness of the preceding target. There was considerable color priming from missed targets. These findings demonstrate relatively intact priming of visual search by color and location in patients with right parietal damage, and also reveal that location priming may differ from color priming in requiring awareness. ■

INTRODUCTION

Visual neglect is a common and disabling syndrome after unilateral brain damage, particularly after substantial strokes in the right middle cerebral artery territory involving the right peri-sylvian cortex and underlying structures. Neglect patients characteristically often fail to explore, acknowledge, or become aware of the contralesional side of space, and may exhibit such failures despite the absence of primary sensory or motor loss (e.g., Driver, Vuilleumier, & Husain, in press; Halligan, Fink, Marshall & Vallar, 2003; Karnath, Milner & Vallar, 2003; Driver & Vuilleumier, 2001; Heilman, Watson & Valenstein, 1997; for discussions of anatomy, see e.g., Mort et al., 2003; Karnath, Ferber & Himmelbach, 2001; Vallar, 1993). One characteristic manifestation of visual neglect is disturbed visual search. Neglect patients may fail to detect contralesional targets in some search tasks; and may recursively search through elements towards the ipsilesional side, mistakenly treating these as new discoveries rather than previously explored items (e.g., Behrman, Ebert, & Black, 2004; Karnath & Nemeier, 2002; Husain et al. 2001; Wojciulik, Husain, Clarke, & Driver, 2001; Behrman, Barton, Watt, & Black, 1997; Eglin, Robertson, & Knight, 1989).

Despite these many deficits, research on neglect has uncovered some residual functions that can survive despite the lesion and the associated deficits in awareness (e.g., see Driver, Vuilleumier, & Husain, in press; Berti, 2003; Driver & Vuilleumier, 2001, for reviews). The presence, color, shape, and even the identity or category of neglected or extinguished objects may still be unconsciously extracted by intact brain structures in the patients' visual system; for example, in the striate, extrastriate, and ventral visual cortex (e.g., see Mattingley et al., 1997; Marzi et al., 1996; Cohen, Ivry, Rafal, & Cohen, 1995; Baylis, Rafal, & Driver, 1993; McGlinchey-Berroth et al., 1993; Berti & Rizzolatti, 1992; Driver, Baylis, & Rafal, 1992; Audet, Bub, & Lecours, 1991). Thus, a contralesional stimulus which escapes awareness can still influence performance in response to a detected ipsilesional item that bears some relation to the neglected item, thus demonstrating that the related property must have been extracted to some extent. Such residual processing has since been observed in studies using ERP or fMRI. Striate and extrastriate areas in the ventral temporal cortex can still be activated to some extent by a visual stimulus that escapes awareness due to extinction or neglect. By contrast, activation of cortical areas in dorsal parietal pathways of the intact hemisphere was found only for consciously seen stimuli (e.g., Driver, Vuilleumier, Eimer, & Rees, 2001; Marzi et al., 2001; Rees et al., 2000, 2002; Vuilleumier et al., 2001, 2002).

¹University College London, ²University Medical Center, Geneva, ³Imperial College, London

Despite these many demonstrations of residual visual processing in neglect patients, few, if any, studies have looked at whether residual functions, such as priming, might *beneficially* influence some of the pathological deficits that the patients exhibit. Here we examined whether neglect patients can still show patterns of priming in a visual search task that may benefit their performance. This allowed us to examine whether any residual functions in neglect patients may influence their search performance despite time delays between successive trials and despite the presence of distracting stimuli, and whether this may have differential effects for different visual properties (i.e., location and color).

Specifically, we examined priming of “popout” search, by repeating the color and/or location of a singleton target over successive trials during the same search task. We used an adapted version of a paradigm originally introduced by Maljkovic and Nakayama (1994, 1996) to study priming in normal visual search (see also Nakayama, Maljkovic, & Kristjánsson, 2004; Wang, Kristjánsson, & Nakayama, in press; Kristjánsson, Wang, & Nakayama, 2002; Goolsby & Suzuki, 2001; Hillstrom, 2000). In a large number of trials with a small number of normal observers (typically $n = 2$), Maljkovic and Nakayama observed strong priming effects on response times from repeating a particular color for a popout target, and also from repeating its particular location. Here we used a similar experimental approach in detailed testing of two neglect patients, to determine whether priming of popout search by color and/or location could occur in patients with right parietal lesions and left neglect; whether this could benefit their impaired search performance; and whether priming could be found from (and to) targets on the contralateral side of space.

In our task, an odd-colored target diamond had its notch removed at top or bottom, rather than on left or right as in Maljkovic and Nakayama (1994), to prevent possible “object-based” neglect for notches on the left side of each target from becoming an issue (see e.g., Pavlovskaya et al., 2002; Driver, 1999; Buxbaum & Farah, 1997). The three diamonds were presented at upper, left, and right positions (see Figure 2), and the singleton target could appear on any one of them in Experiments 1 and 2 (but only on the left or right in Experiment 3). We were particularly interested in comparing performance for ipsilesional and contralesional targets, and in examining any priming arising *from* each particular side, and (in the case of color) potentially *affecting* either side (location priming could only affect the primed location by definition). To our knowledge, no previous study has examined “priming of popout search” in neglect patients as here. One study by Marangolo, Di Pace, Rafal, and Scabini (1998) did examine color priming for neglect patients (see also Cohen et al., 1995), but in a very different go/no-go paradigm which we consider in our Discussion.

RESULTS

Patients

Two patients (both 55 years old) were tested several times, 2–5 months after stroke. On the first occasion, both showed clear signs of left neglect as measured by Mesulam shape-cancellation (patient DO: 10% correct on left side, 77% on right; patient CN: 7% left, 100% right) and BIT star cancellation tasks (patient DO: 7% left, 81% right; patient CN: 7% left, 70% right), and line bisection (patient DO: 1.5 cm right deviation; patient CN 0.5 cm right deviation, both on 20 cm line); and demonstrated visual extinction on confrontation (Mesulam, 1999). The experiments were run in the order that they are presented and by the time of the final experiment their neglect had improved somewhat, but they continued to show strong left visual extinction when stimuli were presented bilaterally, and some neglect (Mesulam shape-cancellation: DO, 85% correct on left side, 96% on the right; CN, 71% correct on left side, 97% on the right; line bisection: DO, 1.2 cm right deviation; CN, 1.1 cm right deviation). Both patients had intact visual fields on confrontation.

Patient DO had suffered a right fronto-parietal infarct (Figure 1A), whereas patient CN had a right hemisphere hematoma centered around the sylvian fissure, extending to the thalamus and lentiform nucleus (Figure 1B). Figure 1C shows the overlap in the lesions of the two patients in black, whereas the white areas are regions damaged in just one of the patients. The area of lesion-overlap centered around the deep white matter of the inferior parietal lobule (IPL) and the superior temporal gyrus (STG). Both patients had structurally intact visual cortex and frontal eye fields (FEFs).

Experiment 1: Priming of Popout Visual Search in Free Vision

The task was to find the uniquely colored diamond (see Figure 2) on each trial and then report by keypress, as quickly as possible, whether it had a notch cutoff at its *top* or *bottom*. A shift of attention towards the singleton target was required for accurate task performance. Over successive trials, the target location could unpredictably remain the same or change, and likewise for its color, in an orthogonal fashion between the two features (determined randomly from trial to trial). Although our main interest was in determining whether priming would be present or absent from (and to) contralesional targets in the patients, we also ran three neurologically intact elderly controls for completeness. Note that, just as in Maljkovic and Nakayama’s (1994) study of two normals, we collected data for a large number of trials in few individuals, rather than brief testing of many individuals. Accuracy was very high for both patients and normals (see below), with the critical results in this study of speeded performance arising from the response times

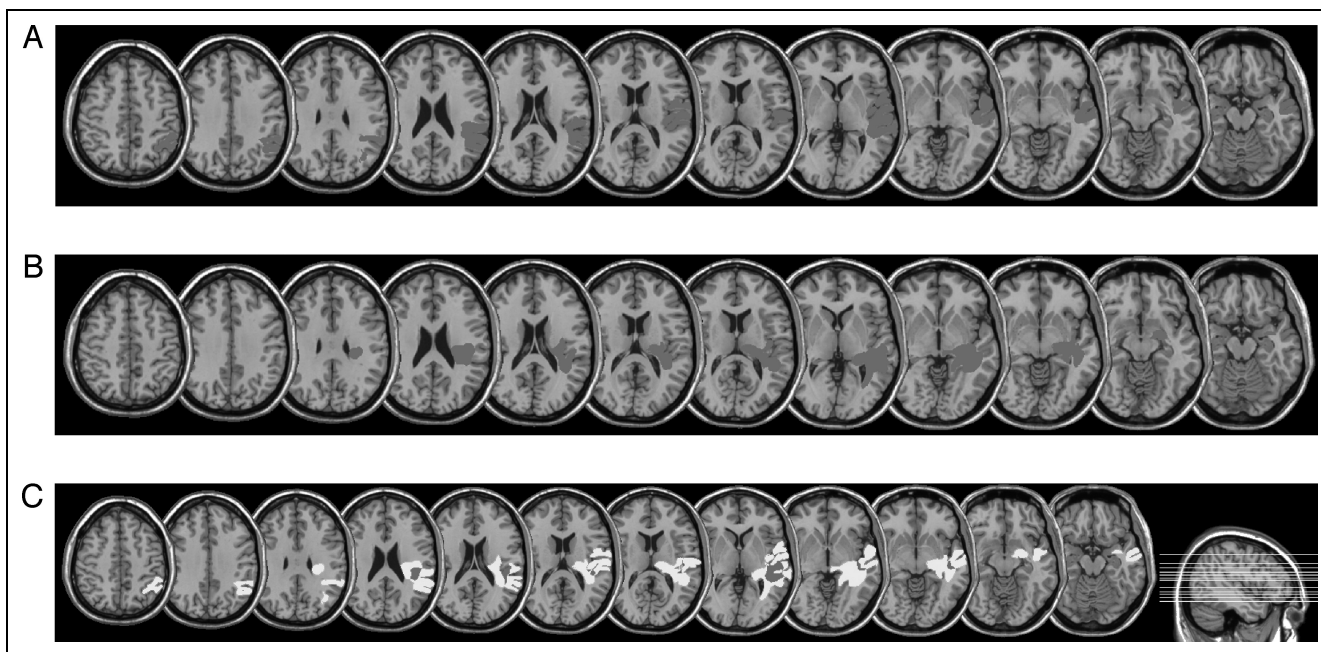


Figure 1. Axial slices showing in black the extent of the lesions for patient DO (A) and CN (B). The overlap in the lesions for the two patients (C) shown in black, with white regions denoting areas specific to only one patient's lesion (note that right in figure shows the right part of the brain). Note that visual and ventral temporal visual pathways, as well as the FEFs were structurally intact in both patients.

(see Figure 3). Both patients showed considerable priming of search performance in reaction time (RT) when target color or location was repeated across successive trials (as did the age-matched controls), although the patients were slower overall, especially for left targets (Figure 3). When target position was repeated, RT became faster relative to when the current target was in a different location than the preceding trial, regardless of color (see Figure 3A). Similarly, responses were speeded if target color was repeated across successive trials, regardless of location (Figure 3B).

ANOVAs were carried out on the individual RTs for each of the patients and for the control observers, with variation between trials providing the error term. Here we analyzed color priming separately for different *current* target locations (given the substantial differences in overall performance for left vs. right targets in neglect patients, and our interest in whether any priming could be found *to* or *from* left targets in these patients). Likewise, our analyses of location priming considered different current locations separately in the patients. ANOVA across trials, with factors of *position* repetition and current position of target, revealed significant main effects of position repetition on the speed of performance within each of the patients [for patient CN: $F(2,487) = 9.45, p < .001$; and for patient DO: $F(2,419) = 3.55, p < .03$], with each of the normal controls also individually showing similar effects or trends [S_1 : $F(2,298) = 3.17, p = .042$; S_2 : $F(2,295) = 2.87, p = .057$; S_3 : $F(2,289) = 2.56, p = .069$]. Unsurprisingly, the patients each also showed a main effect of cur-

rent target location with slower performance for left targets [CN: $F(2,487) = 21.8, p < .001$ and DO: $F(2,419) = 24.49, p < .001$], a pattern that was absent in the normal controls (all F values < 1 , and all p values $> .3$). Importantly, there was no interaction between position priming and target location in any of the observers [CN: $F(4,487) = .71, p = .58$; DO: $F(4,419) = .54, p = .71$; for controls: all F values < 1 , and all p values $> .5$]. Thus, for both neglect patients, priming by repeated target location was found similarly at the left location as for the other locations, despite the patients showing significantly slower performance overall for left targets.

ANOVA on *color* repetition by current target location revealed a significant main effect of color priming for both patients [CN: $F(2,487) = 4.15, p = .016$; DO: $F(2,419) = 11.12, p < .001$] as well as for each control observer [S_1 : $F(2,298) = 2.96, p = .051$; S_2 : $F(2,295) = 4.16, p = .023$; S_3 : $F(2,289) = 2.97, p = .052$]. The Color priming \times Current target location interaction did not approach significance for any of the observers [CN: $F(4,487) = .14, p = .97$; DO: $F(4,419) = .93, p = .45$; for controls: all F values < 1 , and all p values $> .3$], implying that the effect of color priming was similar regardless of the current location of the target. To examine color priming applying from one location to another in more detail, we next examined color priming in the patients separately for successive trials where color priming could arise from the top or the right *toward* the left side, versus *from* the left toward the top or right. Figure 3C reveals that similar color priming was observed “from” preceding left targets, as well as “to”

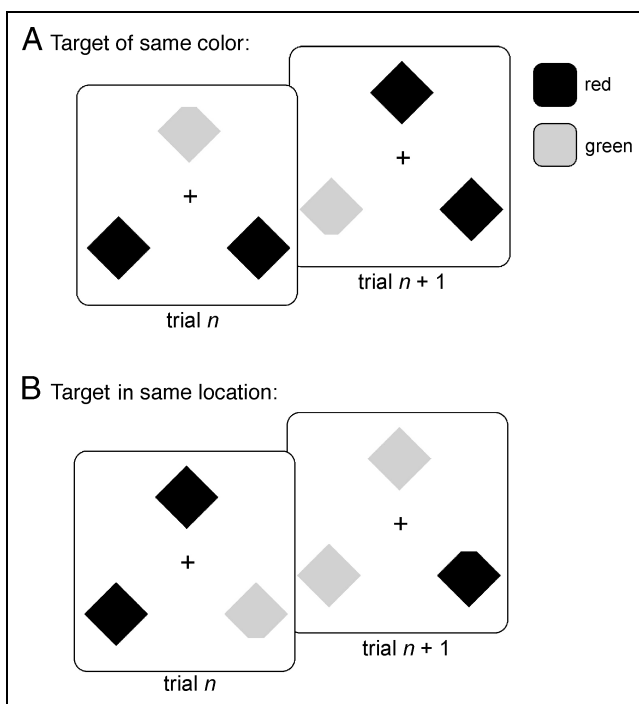


Figure 2. Example sequences of two successive displays illustrating the stimuli and task for Experiment 1. Observers had to indicate as fast as they could whether the uniquely colored target on each trial had a notch removed from its top or bottom (regardless of its location). The other two diamonds had the same color as each other, thus defining them as nontargets. Shown are examples of two consecutive trials where (A) the target is of the same color on these two trials; or (B) where the target is in the same location on two successive trials.

subsequent left targets, in the patients. The color priming pattern between different locations was significant for CN for both priming from top or right to the left [$F(2,115) = 4.71, p = .35$] as well as for priming from the left to the top or to the right [$F(2,115) = 3.97, p = .34$]. For DO the results were similar; priming from the left to the top or right reached significance [$F(2,124) = 5.61, p = .006$], whereas the color priming from the top or right to the left showed a substantial trend [$F(2,124) = 2.94, p = .053$]. Incorrect responses occurred for patient DO on only 5.9%, 3.9%, and 4.3% of singleton targets at the left, right, or top, respectively. For patient CN, the same error rates were 9.6%, 5.3%, and 3.2%; while for the controls the same mean error rates were 0.8%, 1.1%, and 1.4%.

Taken together, the results from Experiment 1 provide initial evidence that color and position “priming of popout” can still be observed for the affected hemifield in neglect. This suggests that the neural pathways supporting such priming of visual search may still be intact to some extent, despite the lesion and despite symptoms of left neglect. Moreover, such priming can evidently benefit the speed of search performance for a target on the impaired contralesional side, thus indicating that it might be of potential benefit in helping to

overcome some of the patients’ deficits. However, one potential criticism of the *location* priming revealed in Experiment 1 is that it might, in principle, just reflect that the patients’ gaze tended to linger at the location of the preceding target, thus benefiting any subsequent target presented there in purely retinal terms. It is possible that the *position* priming observed in the experiment is partly due to lingering of gaze at the location of the last target (although note that this would not, of course, explain the color priming reliably observed between different locations).

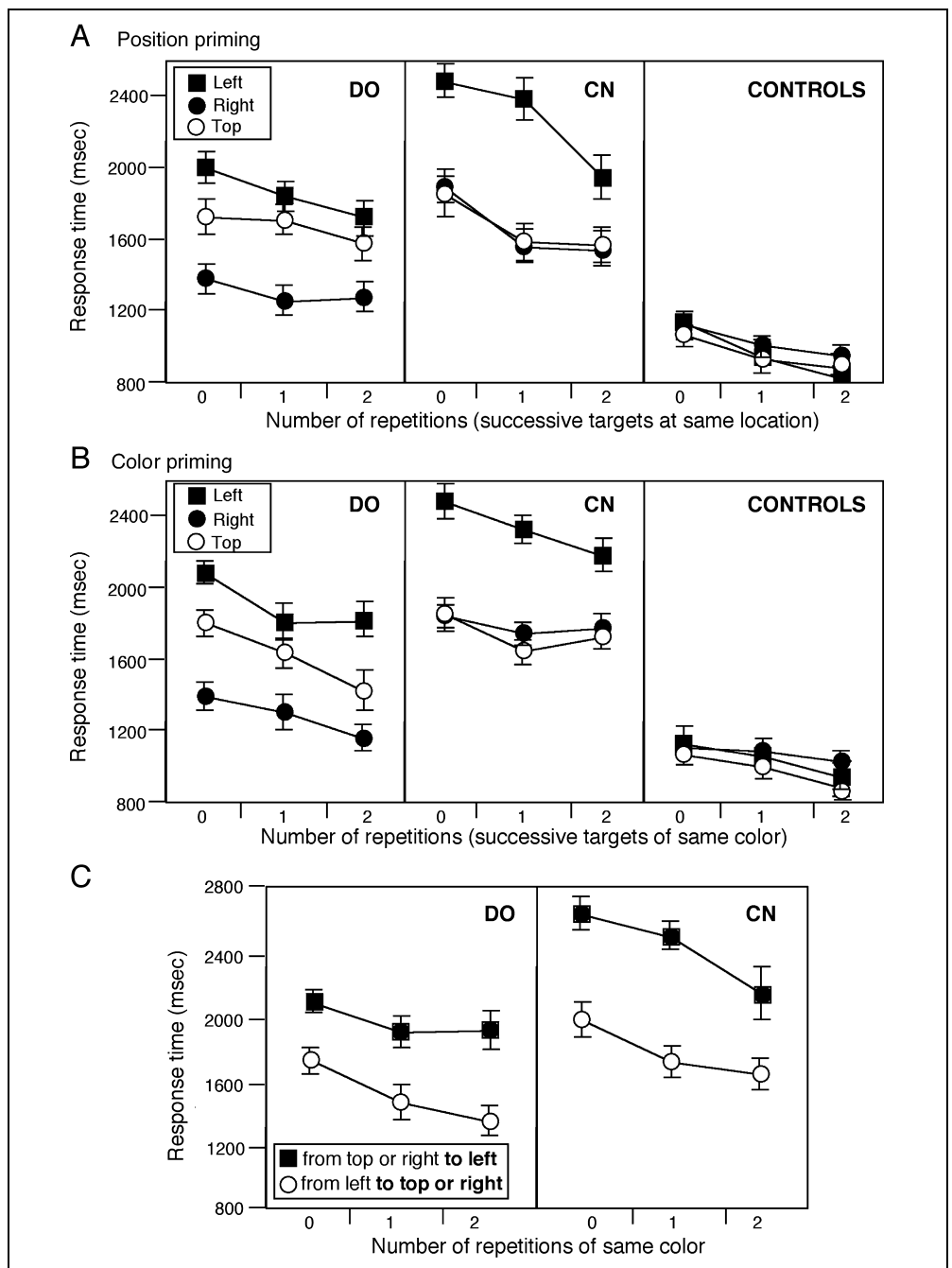
Experiment 2: Priming-of-Popout with Return to Central Fixation between Trials

Experiment 2 addressed the potential lingering-of-gaze issue for location priming, by introducing a letter identification task at fixation before each trial. The letter was too small to be identified with peripheral vision (height 0.5°; see Methods). In order to identify the letter successfully, observers therefore needed to reorient their gaze to the center of the screen for the start of each trial, ensuring that gaze returned to the center between trials. Thus, it was no longer possible for gaze to linger at the peripheral location of the preceding target.

Performance in Experiment 2 (see RT plots in Figure 4) was very similar to that for Experiment 1 (compare Figures 3 and 4), despite the addition of the central letter-discrimination task. Thus, although the time intervals between two successive targets in the search task were even longer and separated by a different intervening stimulus, both patients again showed considerable position and color priming (Figure 4), as did the controls. Moreover, the color priming pattern again generalized across locations, in a similar manner “from” or “to” a left target for the patients (see Figure 4C), as in Experiment 1 (again compare Figures 3 and 4). This similarity shows that lingering of gaze at the location of a previous target cannot account for the position priming, because the central letter task eliminated this possibility.

The ANOVA analysis of position repetition by current location of target showed a significant main effect of repeating the target position for both patients [for patient CN: $F(2,493) = 5.50, p = .004$; and for patient DO: $F(2,395) = 6.82, p < .001$], as well as for the controls [$S_1: F(2,343) = 5.67, p = .004$; $S_2: F(2,348) = 3.3, p = .034$; $S_3: F(2,341) = 6.03, p = .003$]. The main effect of location of target was again significant for both patients [CN: $F(2,487) = 42.12, p < .001$ and DO: $F(2,395) = 12.78, p < .001$], with slower performance for left targets, but not for the control observers (all F values < 1 , and all p values $> .5$). The interaction between position priming and current target location did not reach significance for patient CN [$F(4,487) = 1.37, p = .245$] nor for the controls (all F values < 1.6 , and all p values over $.2$). Although it did reach significance for patient DO [$F(4,395) = 2.88, p = .23$],

Figure 3. Mean RT results from Experiment 1. (A) The location priming pattern separately for targets at different current locations for each patient individually, as well as the means across the three controls. (B) Analogous dataplots for color priming. (C) The results when separating color priming effects in terms of whether these apply from the top or right to the left (solid symbols), separately from color priming from the left to the top or right (open symbols), for each patient. The error bars show standard errors of the mean. The graph shows performance for 0, 1, or 2 or more repetitions of color or position. See text for more details.

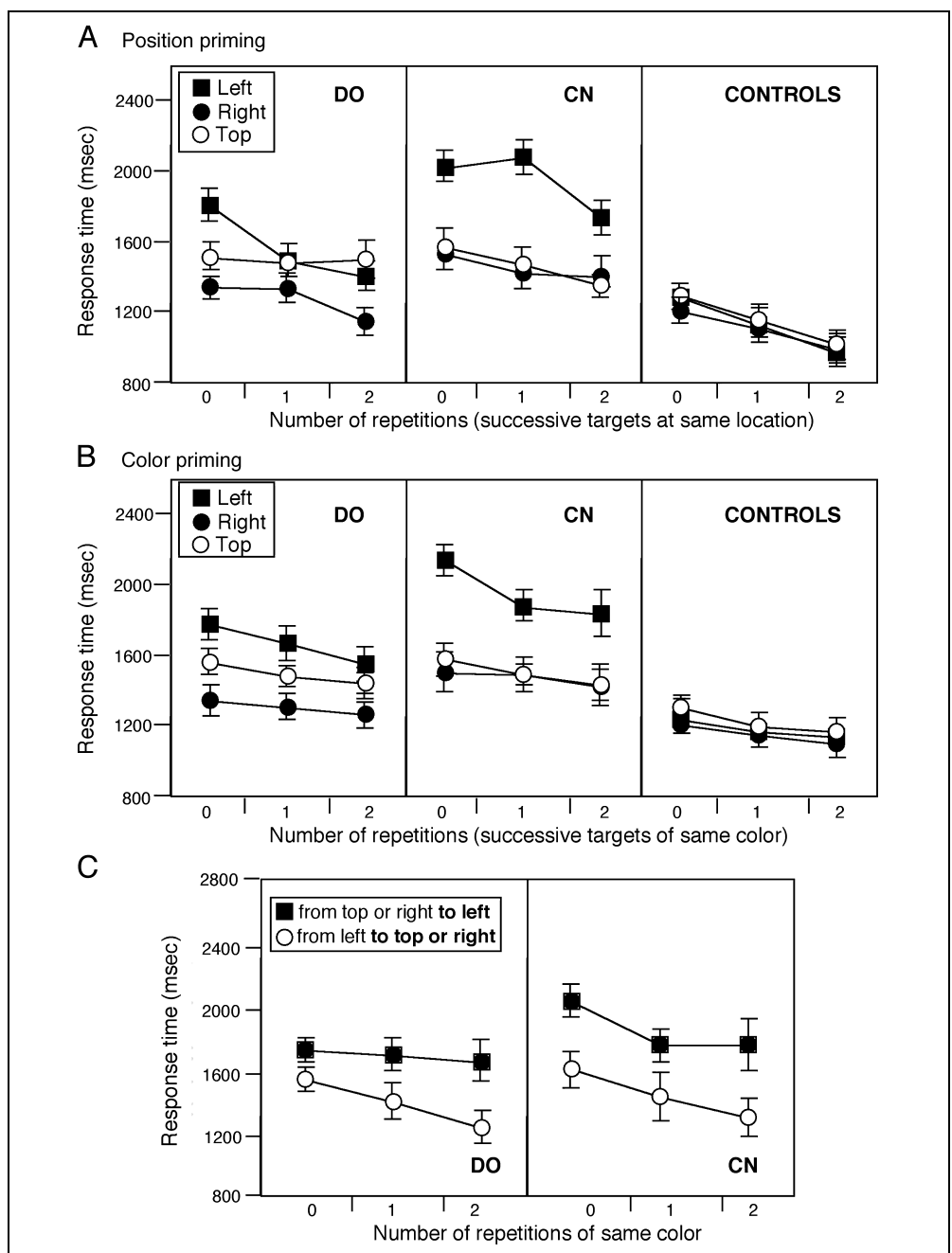


inspection of Figure 4 suggests that this was due to little position priming at the top location for patient DO in this experiment. Although we have no specific explanation for this unexpected detail of the results, we note that the more important finding was reliable position priming for both left [$F(2,129) = 3.70, p = .01$] and right [$F(2,136) = 4.13, p = .008$] targets for both DO and CN (see Figure 4).

The observed position priming pattern was not identical for the two patients (see Figures 3 and 4). Patient CN did not show a consistent position priming effect for left targets until the third successive presentation of a target at the same location (DO showed such a pat-

tern after only one repetition). We will not, however, make much of this apparent difference between patients for several reasons. First, a similar pattern was found in some but not all of the results of Maljkovic and Nakayama (1994, Figure 2; 1996, Figure 11). Second, one of our three normal observers showed a similar pattern of substantial location priming only on the third successive target presentation in a given location. Finally, patient CN did in fact show significant location priming for left targets even with just one repeat in our next experiment. So for present purposes, the most important point of Experiment 2 concerning location priming is that location priming is observed in neglect

Figure 4. Mean RT results from Experiment 2, plotted in the same format as Figure 3 for Experiment 1. (A) The position priming pattern as a function of where the current target appeared (top, right, or left of search display; see key to graph) for each of the two patients, as well as the average for the three elderly controls. (B) An analogous dataplot for color priming. (C) The results for color priming *to* the left from the top or right (solid symbols), or *from* the left to the top or right (open symbols). Standard errors are indicated by error bars. The graph shows performance for 0, 1, or 2 or more repetitions of color or position. See text for more details.



patients, including for left targets, even when central fixation is enforced between successive search trials.

The ANOVAs on color repetition by current target location showed a significant main effect of color repetition for both patients [CN: $F(2,493) = 2.97, p = .037$ and DO: $F(2,395) = 5.01, p = .007$], with similar effects or trends in the controls [$S_1: F(2,343) = 2.11, p = .103$; $S_2: F(2,348) = 3.67, p = .034$; $S_3: F(2,341) = 2.93, p = .054$]. The interaction of color priming and current target location did not approach significance for either of the patients or for the control observers [CN: $F(4,487) = 0.76, p = .555$; DO: $F(4,395) = 0.42, p = .796$; controls: all $F_s < 1.3, p$ values $> .2$].

As in Experiment 1, we looked at the color priming pattern *from* the left side to the top or the right, and from the top and right *to* the left, for the two patients (see Figure 4C). Some color priming was observed for both situations and was significant for patient CN, both for priming from top or right *to* the left [$F(2,124) = 12.31, p = .001$], and for priming *from* left to top or right [$F(2,115) = 6.62, p = 0.012$]. For patient DO, color priming *from* the left to the top or to the right was significant [$F(2,124) = 8.29, p = .005$], but the priming pattern from the top or right *toward* the left did not reach significance [$F(2,124) = 1.23, p = .239$]. DO made errors on only 3.9%, 2.7%, and 3.3% of trials at the left,

right, or top, respectively. For patient CN, the corresponding error rates were 7.9%, 6.7%, and 3.1%; whereas for the controls the mean error rates were 2.2%, 1.8%, and 0.7%. All were highly accurate in naming the central letter (only 2% errors for DO, 1% for CN, and no errors for the controls).

In summary, Experiment 2 shows a very similar pattern of results to Experiment 1 for priming of popout in visual search, despite the insertion of a secondary letter-identification task that requires central fixation between each successive trial. This rules out the possibility that lingering of gaze at the location of the previous target could have accounted for the location priming effects. Moreover, we again found considerable color priming for both patients, even for left targets.

Experiment 3: Brief Displays and Relationship to Awareness

Taken together, the previous two experiments show that neglect patients show both color and position priming, despite their brain damage, and despite their slower performance overall for contralesional left targets. Given that location priming was observed even for left targets in the patients, and that color priming was reliably observed from left targets, it might seem tempting to suggest that such priming can arise even from *neglected stimuli*. However, it should be noted that in Experiments 1 and 2, the patients never failed to detect left targets (the display was visible until the response, and the observers were to search the three locations until the target was found). The patients' contralesional deficit was thus apparent in the previous two experiments only in terms of delayed responses to leftward targets, *not* in a complete failure to become aware of them.

In our final experiment, we studied the possible role of awareness more directly, by using much briefer (200 msec) displays that were most likely too short to permit exploratory saccades, especially for neurological patients, and that might also be sufficiently brief to induce complete perceptual extinction for left targets on some trials (see Figure 5 for the new stimulus procedure; see Methods for further details). Importantly, we now asked the patients to indicate explicitly on each trial whether they had consciously detected a singleton target. Thus, whereas previously the only permissible responses had been “up” or “down” to indicate the notch location, there were now three possible responses: “up,” “down,” or “no target.” Some of the displays (20%) now actually did not contain any singleton color target. The critical dependent variable was thus accuracy.

Instead of merely examining whether priming could occur for left relative to right targets in the patients, as found in Experiments 1 and 2, we could, in principle, also determine whether any such priming would depend on *awareness* of the left item by comparing any priming

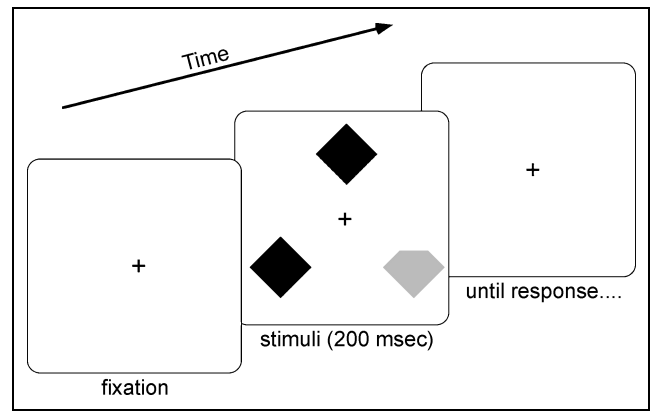


Figure 5. Example trial from Experiment 3. The search display was similar to the previous experiments, but only presented for 200 msec. The notched target could now only appear at the left or right location (never at the top), and was absent on 20% of trials (all three diamonds in the display then had the same color as each other, and none had a notch cutoff).

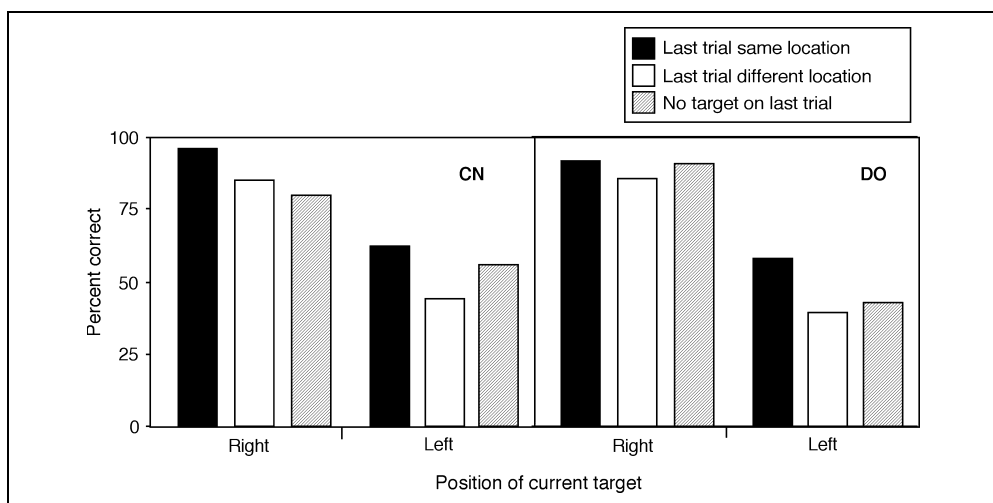
for trials preceded by a detected target; versus by a missed target; and also by comparing each of these situations with trials where no target appeared on the preceding trial.

Display times were now too brief (200 msec) to permit saccades during visual stimulation. The experimenter monitored for central gaze position (instructing the observer to refixate if necessary) before initiating each display. The target on each trial could now only be at the left or right (randomly determined), to ensure sufficient trials of the critical type (i.e., with a left target that might be missed). To allow sufficient power, each patient took part in at least 1400 trials over several sessions.

Our analyses begin by considering accuracy results for the patients in the notch task on target-present trials, regardless of whether the preceding target was detected or escaped awareness. Position priming effects from the preceding trial are shown in Figure 6, regardless of awareness on the preceding trial. Overall, as anticipated, each patient's accuracy in the upper/lower notch task was worse for left than right targets [DO: $\chi^2_{(1)} = 37.8$, $p < .001$; for CN: $\chi^2_{(1)} = 28.9$, $p < .001$]. Importantly, performance was better when the target occupied the same location as the preceding one. This priming pattern was significant for left targets [DO: $\chi^2_{(1)} = 15.09$, $p < .001$; CN: $\chi^2_{(1)} = 14.54$, $p < .001$]. It was also significant for right targets for patient CN [$\chi^2_{(1)} = 12.41$, $p = .002$], with a similar trend for patient DO [$\chi^2_{(1)} = 3.62$, $p = .163$] that did not quite reach significance.

The overall *color* priming effects for the patients are shown in Figure 7. For left targets (Figure 7A), color priming was observed for both patients—performance was better if the color of the current target matched that from the preceding trial (irrespective of location). χ^2 tests confirmed that this pattern was significant in both patients for priming *from* left targets [DO: $\chi^2_{(1)} = 23.77$,

Figure 6. Accuracy in Experiment 3 is shown separately for the two patients (CN and DO) as a function of the location of the current target (left or right, see abscissa) and whether the target was in the same location as on the last trial or not (see key). The dark bars show performance when the last target was in the same location as the present one, the white bars show performance when the last target was in the other location, and the gray bars show performance when there was no target present on the preceding trial.



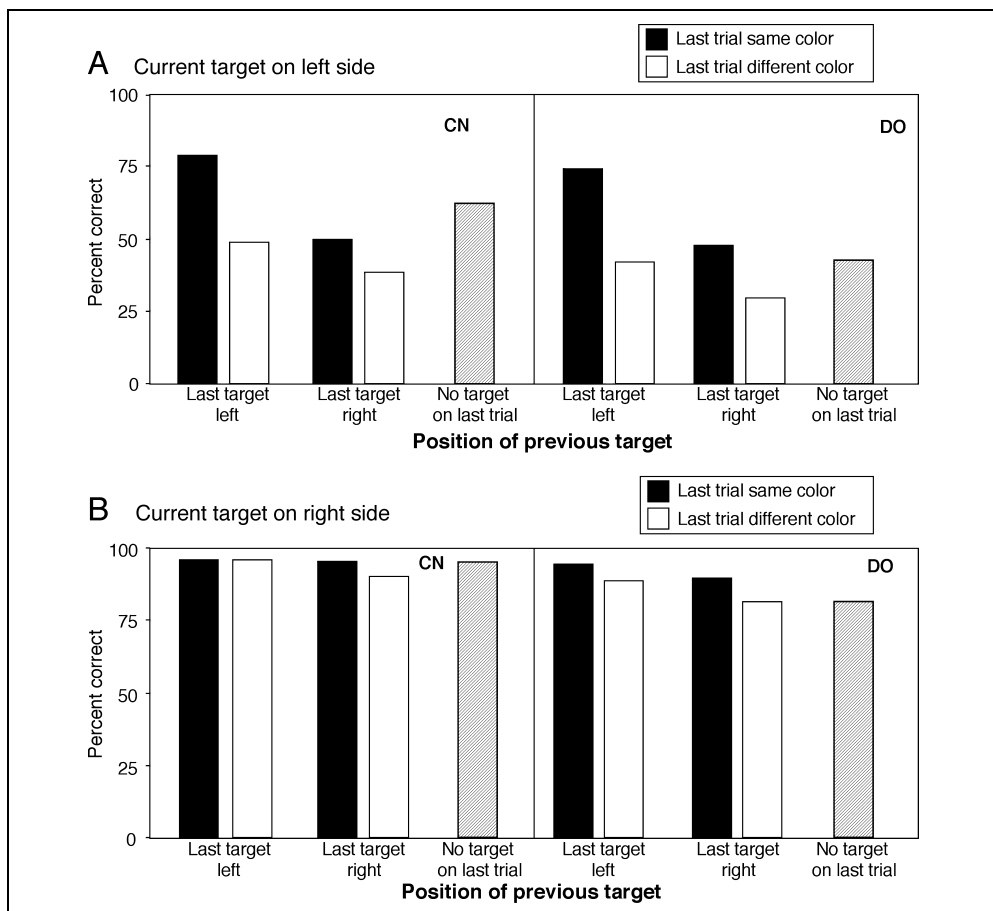
$p < .001$; CN: $\chi^2_{(1)} = 23.33, p < .001$], and for priming from right targets to left targets in DO [$\chi^2_{(1)} = 7.16, p = .028$], but not in CN [$\chi^2_{(1)} = 2.78, p = .249$], although the trend was in the same direction. Figure 7B shows analogous data but now for targets on the right side. Here performance of both patients was close to ceiling, so no significant priming on accuracy could be found (all χ^2 values < 1.9), although any small

trends indicated improved performance with target color repetition.

Is Awareness of a Preceding Left Target Necessary for Priming-of-Popout by it?

To assess whether priming-of-popout search can take place even from a preceding target that has escaped

Figure 7. Accuracy in Experiment 3 shown separately for the two patients, as a function of the location of the current target (A: on the left; B: on the right), and also now as a function of whether the current target had the same or different color as the preceding target (if any). The dark bars show performance when the preceding target had the same color as the present one, and the white bars show performance when the preceding target had a different color from the current target; the hatched bars are for trials where the preceding trial had no target. Note that for left targets (upper graphs), performance was better when the last target had the same color. A location-related cost from having the preceding target on the right side is also apparent for left targets.



awareness, we contrasted patient accuracy where there was *no* target on the previous trial (20% of all trials), versus those where a left target had been *present* and was either detected or missed on the preceding trial. Patient CN missed 49.4% of left visual field targets (but only 5.8% of right field targets); whereas DO missed 52.4% of the left targets (but only 12.4% of right targets).

Figure 8 plots accuracy for current targets presented in the left visual field in the patients, under different preceding conditions, and critically now separated according to whether a preceding left target was detected, missed, or absent. When compared with performance with no target on the previous trial, a *detected* left target on the preceding trial produced location priming (compare first two bars in Figure 8), but a missed target produced none (compare black and gray bars for each patient in Figure 8). This implies that location priming for left targets depended on awareness. Note also, that while a preceding right target (which was almost always detected) led to worse performance for a subsequent left target than with a missed preceding left target (compare third and fourth bars for each patient in Figure 8), this particular effect could be attributed solely to a cost from the preceding right target, rather than to a benefit from a preceding left target.

For position priming, there was a significant difference between left performance when the preceding target was on the right versus on the left for both patients [CN: $\chi^2_{(1)} = 7.82, p = .008$; DO: $\chi^2_{(1)} = 5.96, p = .018$], which can be attributed to a cost from a preceding right target. More importantly, there was a significant difference between performance for a current left target following a preceding detected left target, as compared with no target on the preceding trial [CN: $\chi^2_{(1)} = 12.3, p < .001$; DO: $\chi^2_{(1)} = 9.37, p = .006$]. However, critically

this effect depended on awareness of the preceding left target, being eliminated completely when a left target was missed. Thus, no significant difference was found for preceding missed-left versus no preceding target [CN: $\chi^2_{(1)} = 0.33, p = .62$; DO: $\chi^2_{(1)} = 1.87, p = .149$].

The results were quite different for *color priming*, as shown in Figure 9. Here, accuracy for a current target in the notch task improved when the preceding target had the same color, *even if that preceding target had escaped awareness*, relative to when no target was present on the preceding trial (compare first bar to second and third for each patient in Figure 9; and likewise compare second and third to fourth and fifth bars, and note no differences between the paired white and gray bars). Thus, color priming can arise from missed left targets that escape awareness, whereas position priming instead depends on awareness of the preceding target.

For color priming, χ^2 comparisons critically showed a significant difference between a preceding missed left target with same color as the current target, versus no preceding target [CN: $\chi^2_{(1)} = 9.78, p = .002$; DO: $\chi^2_{(1)} = 6.31, p = .014$]. Likewise, there was a significant difference between preceding missed left targets with same versus different color as the current trial [CN: $\chi^2_{(1)} = 20.31, p < .001$; DO: $\chi^2_{(1)} = 16.96, p < .001$], and likewise following a detected left target on the preceding trial [CN: $\chi^2_{(1)} = 19.07, p < .001$; DO: $\chi^2_{(1)} = 11.64, p = .009$]. The percent correct scores for targets in the right visual field were very high and close to ceiling for both patients (Figure 7B). Probably due to this, differences in performance for the right visual field as a function of preceding target were not significant (all $ps > .05$). The elderly controls were close to ceiling throughout, so no priming analyses could be done for them.

Figure 8. Results from the analysis addressing whether *position* priming effects on accuracy in Experiment 3 depended on awareness of the preceding target. All datapoints in this graph concern performance when the *current* target was on the left. The black bar denotes performance when no target was presented on the preceding trial; the white bars denote performance when a target presented on the previous trial was detected; while the gray bar denotes when the target on the last trial was missed. The latter situation could only be analyzed for missed preceding targets on the left, as there were very few misses on the right (5.8% for CN, 12.4% for DO). Note that accuracy for left targets is enhanced by a preceding detected left targets but not by a preceding missed left target.

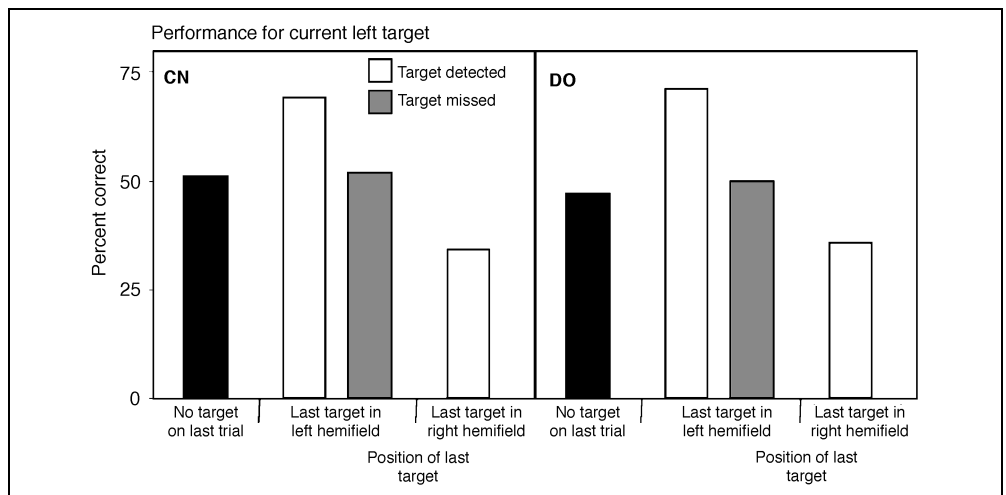
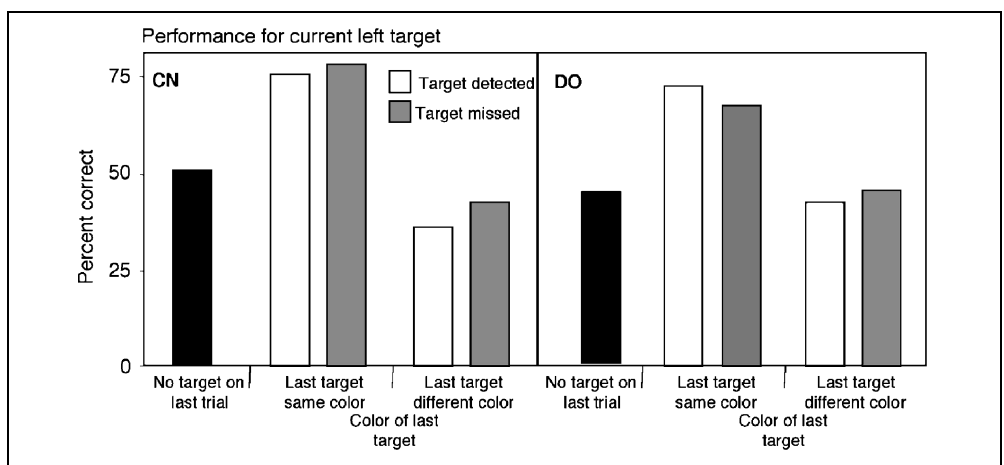


Figure 9. Results from the analysis addressing whether *color* priming effects on accuracy in Experiment 3 depended on awareness of the preceding target. All datapoints in this graph concern performance on trials when the current target, as well as any preceding target, were on the left. The black bar denotes performance when no target was presented on the preceding trial; the white bars denote performance when the target presented on the preceding trial was detected; and the gray bar denotes



performance when the target on the preceding trial was missed. Note that accuracy for left targets is enhanced by a preceding target with the same color compared to no preceding target (black bar) or a target with a different color regardless of whether the preceding target was detected or missed.

In sum, in Experiment 3 we used brief displays so that some of the left targets now escaped awareness in the patients. Priming-of-popout for accuracy was observed for both location and color, but with the critical difference that color priming did not depend on awareness of the preceding left target from which it might arise, whereas location priming clearly did.

DISCUSSION

We have presented the results of three experiments examining in detail priming-of-popout in visual search for two patients with left visual neglect and extinction. The main results of Experiment 1 were that reliable priming by repeated target location, as well as by repeated target color, was found in both patients, occurring *to* and *from* left targets. Indeed, despite this overall slowing for left targets, there was no interaction between either type of priming effect (i.e., repeated target location or color), and the location of the current target in the patients (nor in the controls). This indicates that priming of popout can benefit left-sided targets in the patients to the same extent as at other locations in these search conditions. Thus, priming of visual search can improve patients' performance on their neglected left side; and priming of visual search can also arise from their left side (as for color priming from a left to a top or right target). In Experiment 2, we used a similar paradigm to Experiment 1, except that a secondary task of identifying a small character at display center was now interleaved between successive visual search trials, to ensure that fixation had to return to center prior to the next search display (ruling out that location priming was caused by gaze lingering at the location of the last target). The same pattern of results was obtained as before. Both patients showed reliable color and position priming on the right and left. Thus, even the affected

side benefited from location priming, even after an intervening stimulus between each successive trial.

In Experiment 3, we used brief displays (200 msec) in a similar search task, both to preclude saccades during the presentation of the search display, and to assess whether priming-of-popout might depend on awareness of the preceding target. The patients now failed to detect a left singleton target on approximately 50% of trials. Position priming and color priming affected accuracy in this new search task for each patient. But importantly there was now a dissociation between color and position priming: Although *color* priming occurred regardless of whether a preceding left target had been consciously detected or escaped awareness (Figure 9), *location* priming of popout by a preceding left target depended on awareness of that preceding target, with no such priming occurring when the preceding left target escaped awareness (see Figure 8). To our knowledge, these experiments provide the first investigation of priming-of-popout in patients with left neglect and extinction.

Our finding that color priming occurs regardless of awareness converges well with prior research on neglect (Cohen et al. 1995; see also Driver & Vuilleumier, 2001, for review) that showed "implicit" effects of color from the affected left side, albeit in a flanker-interference task with simultaneous presentation of the prime and probe stimuli, rather than in a visual search task with substantial time intervals between successive events as here. Such effects of color may relate to residual functions of intact regions within the ventral visual pathway, known to be involved in color processing (Bartels & Zeki, 2000; Hadjikhani et al., 1998). Moreover, recent functional imaging studies in neglect/extinction patients have now shown that such ventral regions of the visual cortex can still be activated unconsciously by stimuli on the affected left side that escape awareness (Vuilleumier et al., 2001, 2002; Rees et al., 2000, 2002; see Driver,

Vuilleumier, Eimer et al., 2001 for a review). Such residual activation presumably arises for the missed left targets that could then produce significant color priming of visual search for both patients. Esterman, McGlinchey-Berroth, and Milberg (2000) reported that targets in the affected hemifield do popout against a set of distractors if there is a single unique feature (like color, for example) that distinguishes them from the distractors. It is, however, clear from the findings here that responses of neglect patients to popout targets are slowed (Experiments 1 and 2) and they often miss the popout targets if presentation is too brief (Experiment 3). So even though set size does not have a significant effect on response times for the affected hemifield (Esterman et al. 2000), it is likely that the popout is slowed for targets in the affected hemifield.

Marangolo et al. (1998) reported the only study we are aware of that suggested an *absence* of specific color and location priming effects in a group of posterior parietal patients (most of whom did not have neglect, unlike our patients). However, that study used a very different procedure to the present visual search tasks (which we had selected here on the basis of their successful previous use for studying visual search in normals; cf. Maljovic & Nakayama, 1994, 1996). In the study of Marangolo et al., a go/no-go procedure was used instead of a search task, in which peripheral visual targets had to be detected following a central cue predicting (either validly or invalidly) the color and/or the side of the upcoming targets. Only a single stimulus was presented at a time, with a short interval of just 200 msec between the prime and the subsequent probe. Color and location priming in this paradigm was reportedly absent for probes in the contralesional field in this group of parietal patients. Although we have no specific explanation for their results, it seems possible that responses to a contralesional target following so quickly after a prime may have been rather variable (see also Table 3 in Marangolo et al., where few individual patients seem to show the group mean pattern). However, we note in any case that the paradigms used in the two studies differ in many ways, with their study focusing on reflexive orienting of attention and our study addressing visual search. Most importantly, the Marangolo et al. findings do not in any way undermine the present positive demonstrations, repeated across three separate experiments, of reliable and replicable location and color priming in popout visual search. Moreover, our results show that, in visual search at least, location and color priming can improve performance for left targets, and so reflect some intact mechanisms in attention that could, in principle, be beneficial to such patients in a way that might be exploited in rehabilitation.

One of the most remarkable findings was that although color priming did not depend on awareness of the preceding target in our patients, location priming clearly did (Experiment 3), being observed for both

patients when a preceding left target was detected, but not if it had been missed. Why should location but not color priming depend on awareness? This might seem surprising for those accounts that associate location processing with supposedly “unconscious” dorsal pathways, but color processing with supposedly “conscious” ventral pathways (Goodale, Westwood & Milner, 2004; Milner & Goodale, 1995). Many have, however, shown that some forms of processing in ventral visual pathways can proceed unconsciously, including in neglect (Driver & Vuilleumier, 2001; Vuilleumier et al., 2001; Rees et al., 2000) and blindsight patients (shown with neuroimaging, Goebel, Muckli, Zanella, Singer, & Stoerig, 2001; and with various behavioral measures, see e.g., Stoerig & Cowey, 1997). Nevertheless, the clear association of location priming with awareness here remains intriguing. One possibility is that location priming of visual search is associated with shifts of covert spatial attention, and that the latter are intrinsically linked to awareness (see Driver & Vuilleumier, 2001; Rees & Lavie, 2001 for discussions). In fact, imaging studies in neglect patients (Rees et al., 2002; Vuilleumier et al., 2001) and normal observers (Beck, Rees, Frith & Lavie, 2001; Dehaene & Naccache, 2001) have suggested that some areas within the parietal cortex involved in spatial attention may be activated only during conscious perception of visual stimuli, but not for missed stimuli, even though the latter still activate ventral temporal areas. Another (potentially related) possibility is that the lesions in neglect patients typically disrupt location processing more than color processing, but with the location disruptions operating in a probabilistic manner that can vary from trial to trial rather than applying in a fixed manner (there is usually variability from trial to trial during testing of visual extinction). The trials where a preceding left target was in fact consciously detected might be precisely those where the disruption caused by the lesion was not sufficient to prevent appropriate location processing. Note that whatever the most appropriate theoretical interpretation, our critical empirical finding from Experiment 3 remains that location priming was yoked to awareness, whereas color priming was not, so any future accounts of awareness in neglect should take this new finding into account, although we cannot rule out that cases may be found for whom the position priming is not as clearly dependent on awareness, but the consistency in the results for the two patients is, to our mind, quite persuasive.

Concerning the possible neural bases for the effects on visual search observed here, those aspects of priming-of-popout that were preserved behaviorally clearly imply that (at least some of) the neural pathways for producing location and color priming-of-popout remained intact in our two patients. As discussed above, color priming is likely to involve ventral visual pathways that may then interact with other centers affecting search, and such interactions may persist even without

awareness in the patients. Likewise, location priming must presumably also rely on pathways that survive the patients' lesions (see Figure 2) and are activated by awareness of the target. Bichot and Schall (1999) conducted single-cell studies in awake behaving monkeys performing singleton search tasks similar to those used by Maljkovic and Nakayama (1994, 1996) and our study. They found that neurons in FEF discriminated faster and more reliably between targets and distractors when target color was repeated. Given these results, it may be noteworthy that the likely human homologue of monkey FEF (in and around the precentral sulcus and the superior frontal sulcus; see Paus, 1996) was structurally intact in both our patients (Figure 1). Residual activation in neural pathways coding for color or spatial location information may have been sufficient to influence FEF activity in the patients. It should be of great interest in future work to examine whether any of the priming phenomena examined here are pathologically absent in human patients with FEF lesions (Rafal, Machado, Ro, & Ingle, 2000). Two conference abstracts have reported initial fMRI results from neurologically healthy observers performing priming-of-popout tasks like those used here. Preliminary findings indicate influences of such priming on visual and frontal regions (Kristjánsson, Vuilleumier, Husain, Macaluso, & Driver, 2004; most or all of which were structurally intact in our two neglect patients), in addition to intraparietal areas (Kristjánsson, Wang, et al., 2002; Yoshida et al., 2003). It would be of interest to see whether single neurons in the monkey homologues of regions in humans that show priming-related effects in fMRI do exhibit a similar change in responding as a function of priming as Bichot and Schall (2002) observed for FEF neurons.

In conclusion, our three experiments show that priming-of-popout for visual search, by repeated target location or color, can still operate in neglect patients, and can benefit their performance for targets on the affected side. These effects are preserved even with brief displays that preclude saccades toward the singleton target. Color priming was found regardless of whether a preceding left target escaped the patients' awareness; but by contrast, location priming was clearly yoked to awareness of the preceding left target. These results extend the range of preserved functions that can survive in neglect patients and reveal a critical difference for encoding location and color properties as a function of awareness, and show that significant beneficial effects can be obtained from such residual abilities on visual search performance.

METHODS

Experiment 1

Three diamonds, either red (14.8 cd/m²) or green (13.9 cd/m²), were presented on each trial. If two

of the diamonds were red, the third one was green (Figure 2), and thus served as the singleton target on that trial (and vice versa). Observers were told to find the oddly colored target and decide whether its cutoff (or "notch") was at the top or bottom. The color of the target was determined randomly from trial to trial. They were asked to press the appropriate key (to indicate cutoff at top or bottom) as quickly as possible while trying to avoid making many errors. A white (56.6 cd/m²) fixation cross was visible throughout. The display items were presented on a black (0.5 cd/m²) background. Auditory feedback generated by the computer was given to indicate whether the response was correct or incorrect. An Apple G4 laptop computer with an LCD screen (to enable bedside testing) was used for the stimulus display and feedback, while observers responded on an external keyboard. Viewing distance was kept as close to 67 cm as possible. Thus, the effective size of the diamonds was 2.9° of arc and the cutoff at the top or bottom was 18 min of arc. The search items were 5.8° away from the center of the screen. The search displays remained on the screen until the observer responded after which a new trial started, 1200 to 1600 msec later (determined randomly). Patient DO participated in 450 trials in Experiment 1, whereas patient CN participated in 500 trials. Each of the three elderly controls participated in 300 trials. For all participants, all of the data were collected on the same day (100 trials in each block; except for the last block of 50 trials for patient DO with considerable rest breaks in between, especially for the patients). Trials with incorrect responses were not included in the RT analysis. The controls in Experiment 1 were two women, aged 65 and 62, and 1 man, aged 71. They were neurologically healthy, and showed no hemifield-dependent deficits. The results for the elderly control were very homogenous, hence, we present their averages in Figure 3 (even though separate *F* tests were carried out for each).

Experiment 2

Methods were similar to Experiment 1, except that 1500 msec before the start of each trial, observers had to verbally report the identity of a single upper-case white letter (56.6 cd/m²; Helvetica, sans serif font, 30 arc min) at the center of the screen (we used the 26 letters of the English alphabet). The letter was visible until the observers responded. A pilot test on two experienced psychophysical observers confirmed that they were at chance at the letter discrimination when their gaze was centered on one of three possible target positions.¹ The letter was then replaced with a fixation cross, 1200 to 1600 msec after which a trial commenced which was in every respect similar to Experiment 1. The few trials where letter identity was not reported correctly were excluded (2% for DO, 1% for CN, and 0% for

the control observers). The same two patients were tested as in Experiment 1 and two of the same elderly controls as in Experiment 1 (the man, and the younger woman) as well as a new recruit (a 61-year-old woman). Patient CN was tested on 500 trials, patient DO on 400 trials, and the elderly controls were tested on 350 trials each. For all participants, all of the data were collected on the same day (100 trials in each block; except for the last block for patient CN with considerable rest breaks in between, especially for the patients). Trials with incorrect responses were not included in the RT analysis.

Experiment 3

The stimulus display was similar to Experiment 1 except that the stimulus items were now only visible for 200 msec, after which the screen became blank (see Figure 5). For that reason, the size of the cutoff on the target was slightly increased (from 18 arc min to 25 arc min) as finding the cutoff was now harder. The only possible target locations in Experiment 3 were the left or the right (thus the top diamond now only indicated whether the right or the left diamond was the odd one out). The reason was that we wanted to get as much data as possible for the right and left positions to obtain sufficient power to answer the experimental questions, some of which now specifically focused on priming from missed left targets. In addition, on 20% of the trials, there was *no* singleton target (instead, all three diamonds now shared the same color). This was done to enable us to compare performance on trials following those where no target was presented to performance on trials following those where a target was missed. There were thus three response possibilities in this experiment: “up” or “down,” indicating whether the target had a cutoff at the top or bottom, or “no-target” indicating that no singleton target had been detected. The observers were forced to guess about whether the cutoff was upper or lower, if they thought that they had seen a singleton target.

The same two patients as before were tested. A large number of trials were needed for each observer for sufficient statistical power. For that reason, patient CN participated in 1450 trials and patient DO participated in 1400 trials. They were tested on three separate occasions over a 2-week period (for patient DO) and a 4-week period for CN. A χ^2 test over the three sessions revealed that there was no significant change in performance for the left visual field over the three testing sessions for either patient [for DO: $\chi^2_{(2)} = 1.31, p > .05$; for CN: $\chi^2_{(2)} = 0.98, p > .05$]. The same three elderly controls as in Experiment 2 were tested. Only 400 trials for each of them were needed to establish that they were at ceiling on the task.

Acknowledgments

AK was supported by a long-term fellowship from the Human Frontiers Science Program and JD was supported by grants from the MRC and the Wellcome Trust.

Reprint request should be sent to Árni Kristjánsson, Institute of Cognitive Neuroscience, 17, Queen Square, London, WC1N 3AR, UK, or via e-mail: a.kristjansson@ucl.ac.uk.

Note

1. Both subjects participated in 200 trials and S1 responded correctly on 6 of the 200 trials (3% correct) and S2 responded correctly on 11 of the 200 trials (5.5% correct). Chance performance is 3.84% correct.

REFERENCES

- Audet, T., Bub, D., & Lecours, A. R. (1991). Visual neglect and left-sided context effects. *Brain & Cognition, 16*, 11–28.
- Bartels, A., & Zeki, S. (2000). The architecture of the colour centre in the human visual brain: New results and a review. *European Journal of Neuroscience, 12*, 172–193.
- Baylis, G., Rafal, R., & Driver, J. (1993). Visual extinction and stimulus repetition. *Journal of Cognitive Neuroscience, 5*, 453–466.
- Beck, D. M., Rees, G., Frith, C., & Lavie, N. (2001). Neural correlates of change detection and change blindness. *Nature Neuroscience, 4*, 645–650.
- Behrmann, M., Barton, J. J. S., Watt, S., & Black, S. E. (1997). Impaired visual search in patients with unilateral neglect: An oculographic analysis. *Neuropsychologia, 35*, 1445–1458.
- Behrmann, M., Ebert, P., & Black, S. E. (2004). Hemispatial neglect and visual search: A large scale analysis. *Cortex, 40*, 247–263.
- Berti, A. (2003). Unconscious processing in neglect. In H. O. Karnath, A. D. Milner & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect*. Oxford: Oxford University Press.
- Berti, A., & Rizzolatti, G. (1992). Visual processing without awareness: Evidence from unilateral neglect. *Journal of Cognitive Neuroscience, 4*, 345–351.
- Bichot, N. P., & Schall, J. D. (1999). Effects of similarity and history on neural mechanisms of visual selection. *Nature Neuroscience, 2*, 549–554.
- Bichot, N. P., & Schall, J. D. (2002). Priming in macaque frontal cortex during popout visual search: Feature-based facilitation and location-based inhibition of return. *Journal of Neuroscience, 22*, 4675–4685.
- Buxbaum, L. J., & Farah, M. J. (1997). Object-based attention in visual neglect: Conceptual and empirical distinctions. In H.-O. Karnath & P. Thier (Eds.), *Parietal lobe contributions to orientation in 3D space* (pp. 384–400). Berlin: Springer.
- Cohen, A., Ivry, R., Rafal, R., & Kohn, C. (1995). Response code activation by stimuli in the neglected visual field. *Neuropsychology, 9*, 165–173.
- Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition, 79*, 1–37.

- Driver, J. (1999). Egocentric and object-based visual neglect. In N. K. Burgess & J. O'Keefe (Eds.), *The hippocampal and parietal foundations of spatial cognition*. Oxford: Oxford University Press.
- Driver, J., Baylis, G. C., & Rafal, R. D. (1992). Preserved figure-ground segregation and symmetry perception in visual neglect. *Nature*, *360*, 73–75.
- Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, *79*, 39–88.
- Driver, J., Vuilleumier, P., Eimer, M., & Rees, G. (2001). Functional magnetic resonance imaging and evoked potential correlates of conscious and unconscious vision in parietal extinction patients. *Neuroimage*, *14*, S68–S75.
- Driver, J., Vuilleumier, P., & Husain, M. (2004). Spatial neglect and extinction. In M. Gazzaniga (Ed.), *The new cognitive neurosciences III* (pp. 589–606). Cambridge: MIT Press.
- Eglin, M., Robertson, L. C., & Knight, R. T. (1989). Visual search performance in the neglect syndrome. *Journal of Cognitive Neuroscience*, *1*, 372–385.
- Esterman, M., McGlinchey-Berroth, R., & Milberg, W. (2000). Preattentive and attentive visual search in individuals with hemispatial neglect. *Neuropsychology*, *14*, 599–611.
- Goebel, R., Muckli, L., Zanella, F. E., Singer, W., & Stoerig, P. (2001). Sustained extrastriate cortical activation without visual awareness revealed by fMRI studies of hemianopic patients. *Vision Research*, *41*, 1459–1474.
- Goodale, M. A., Westwood, D. A., & Milner, A. D. (2004). Two distinct modes of control for object-directed action. *Progress in Brain Research*, *144*, 131–144.
- Goolsby, B. A., & Suzuki, S. (2001). Understanding priming of color-singleton search: Roles of attention at encoding and “retrieval”. *Perception & Psychophysics*, *63*, 929–944.
- Hadjikhani, N., Liu, A. K., Dale, A. M., Cavanagh, P., & Tootell, R. B. (1998). Retinotopy and colour sensitivity in human visual cortical area V8. *Nature Neuroscience*, *1*, 235–241.
- Halligan, P. W., Fink, G. R., Marshall, J. C., & Vallar G. (2003). Spatial cognition: Evidence from visual neglect. *Trends in Cognitive Sciences*, *7*, 125–133.
- Heilman, K. M., Watson, R. T., & Valenstein, E. (1997). Neglect: Clinical and anatomical aspects. In M. J. Farah (Ed.), *Behavioral neurology and neuropsychology* (pp. 309–317). New York: McGraw-Hill.
- Hillstrom, A. P. (2000). Repetition effects in visual search. *Perception and Psychophysics*, *62*, 800–817.
- Husain, M., Mannan, S., Hodgson, T., Wojciulik, E., Driver, J., & Kennard, C. (2001). Impaired spatial working memory across saccades contributes to abnormal search in parietal neglect. *Brain*, *124*, 941–952.
- Karnath, H., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature*, *411*, 951–953.
- Karnath, H. O., Milner, A. D., & Vallar, G. (2003). *The cognitive and neural bases of spatial neglect*. Oxford: Oxford University Press.
- Karnath, H. O., & Nemeier, M. (2002). Task-dependent differences in the exploratory behaviour of patients with spatial neglect. *Neuropsychologia*, *40*, 1577–1585.
- Kristjánsson, Á., Vuilleumier, P., Husain, M., Macaluso, E., & Driver, J. (2004). Neural correlates of priming in vision: Evidence from Neuroimaging and Neuropsychology. *Perception*, *33*, 13a.
- Kristjánsson, Á., Wang, D., & Nakayama, K. (2002). The role of priming in conjunctive visual search. *Cognition*, *85*, 37–52.
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, *22*, 657–672.
- Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. Role of position. *Perception & Psychophysics*, *58*, 977–991.
- Marangolo, P., Di Pace, E., Rafal, R., & Scabini D. (1998). Effects of parietal lesions in humans on color and location priming. *Journal of Cognitive Neuroscience*, *10*, 704–716.
- Marzi, C. A., Girelli, M., Natale, E., & Miniussi, C. (2001). What exactly is extinguished in unilateral visual extinction? Neurophysiological evidence. *Neuropsychologia*, *39*, 1354–1366.
- Marzi, C. A., Smania, N., Martini, M. C., Gambina, G., Tomelleri, G., Palamara, A., Alessandrini, F., & Prior, M. (1996). Implicit redundant-targets effect in visual extinction. *Neuropsychologia*, *34*, 9–22.
- Mattingley, J. B., Davis, G., & Driver, J. (1997). Preattentive filling-in of visual surfaces in parietal extinction. *Science*, *275*, 671–674.
- McGlinchey-Berroth, R., Milberg, W. P., Verfaellie, M., Alexander, M., & Kilduff, P. T. (1993). Semantic processing in the neglected visual field: Evidence from a lexical decision task. *Cognitive Neuropsychology*, *10*, 79–108.
- Mesulam, M. M. (1999). Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, *354*, 1325–1346.
- Milner, D., & Goodale, M. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Mort, D. J., Malhotra, P., Mannan, S. K., Rorden, C., Pambakian, A., Kennard, C., & Husain, M. (2003). The anatomy of visual neglect. *Brain*, *126*, 1986–1997.
- Nakayama, K., Maljkovic, V., & Kristjánsson, A. (2004). Short term memory for the rapid deployment of visual attention. In M. Gazzaniga (Ed.), *The new cognitive neurosciences III* (pp. 397–408). Cambridge: MIT Press.
- Paus, T. (1996). Location and function of the human frontal eye-field: A selective review. *Neuropsychologia*, *34*, 475–483.
- Pavlovskaya, M., Ring, H., Groswasser, Z., & Hochstein, S. (2002). Searching with unilateral neglect. *Journal of Cognitive Neuroscience*, *14*, 745–756.
- Rafal, R., Machado, L., Ro, T., & Ingle, H. (2000). Looking forward to looking: What can functional imaging reveal about the role of attention in visual awareness? *Neuropsychologia*, *39*, 1343–1353.
- Rees, G., & Lavie, N. (2001). What can functional imaging tell us about the role of attentional load in awareness? *Neuropsychologia*, *39*, 1343–1353.
- Rees, G., Wojciulik, E., Clarke, K., Husain, M., Frith, C., & Driver, J. (2000). Unconscious activation of visual cortex in the damaged right hemisphere of a parietal patient with extinction. *Brain*, *123*, 1624–1633.
- Rees, G., Wojciulik, E., Clarke, K., Husain, M., Frith, C., & Driver, J. (2002). Neural correlates of conscious and unconscious vision in parietal extinction. *Neurocase*, *8*, 387–393.
- Stoerig, P., & Cowey, A. (1997). Blindsight in man and monkey. *Brain*, *120*, 535–559.
- Vallar, G. (1993). The anatomical basis of spatial neglect in humans. In I. H. Robertson & J. C. Marshall (Eds.), *Unilateral neglect: Clinical and experimental studies* (pp. 27–62). Hillsdale, NJ: Erlbaum.

- Vuilleumier, P., Armony, J. L., Clarke, K., Husain, M., Driver, J., & Dolan, R. J. (2002). Neural response to emotional faces with and without awareness: Event-related fMRI in a parietal patient with visual extinction and spatial neglect. *Neuropsychologia*, *40*, 2156–2166.
- Vuilleumier, P., Sagiv, N., Hazeltine, E., Poldrack, R. A., Swick, D., Rafal, R. D., & Gabrieli, J. D. E. (2001). Neural fate of seen and unseen faces in visuospatial neglect: A combined event-related functional MRI and event-related potential study. *Proceedings of the National Academy of Sciences, U.S.A.*, *98*, 3495–3500.
- Wang, D., Kristjánsson, A., & Nakayama, K. (in press). Efficient visual search without top-down or bottom-up guidance. *Perception & Psychophysics*.
- Wojciulik, E., Husain, M., Clarke, K., & Driver, J. (2001). Spatial working memory deficit in unilateral neglect. *Neuropsychologia*, *39*, 390–396.
- Yoshida, T., Tsubomi, H., Osaka, M., & Osaka, N. (2003). Priming of pop-out—An fMRI study. *Perception*, *32*, 93c.