 Implicit representation and explicit detection of features in patients with hemispatial neglect

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Despite profound inattention to the side of space opposite a brain lesion in patients with unilateral neglect, priming studies demonstrate that undetected stimuli are capable of influencing subsequent behaviour. However, the nature of implicit processing of neglected stimuli is poorly understood. In the current study, we examined implicit processing in five patients with neglect using both visual search and priming methods. A psychophysical staircase method varying time of presentation was first used to establish a high (75%) and low (25%) detection probability for targets in both a feature and a conjunction search array. The arrays were then used in a priming task to examine how a difference in the level of overt detection of a feature or a conjunction presented in neglected space influenced subsequent discrimination speed to a single probe presented at fixation. The results showed that priming effects with feature primes were independent of their explicit detection rates (high versus low), but priming effects with conjunction primes reflected the pattern of explicit detection. These findings are discussed as they relate to availability versus accessibility of neglected stimuli.

Keywords: neglect; attention; preconscious; feature; conjunction

Despite profound inattention to the side of space opposite a brain lesion in patients with unilateral neglect, priming studies demonstrate that undetected stimuli are capable of influencing subsequent behaviour (see Driver and Vuilleumier, 2001 for review). For example, an undetected picture of a baseball bat presented in an area of space that patients may deny even exists can, nonetheless speed response to the subsequent presentation of the word ‘ball’ compared to an unrelated word (McGilinche-Berroth et al., 1993). The ‘undetected’ stimulus primes the response to the detected stimuli even when the priming event goes unnoticed. However, prior studies often utilized a fixed prime duration (e.g. 600 ms) in patients who exhibit a large variance in levels of awareness. Thus, the degree to which prime stimuli went unnoticed is unknown. Further, prior studies often relied on inquiry following the probe task to determine if patients were aware of the prime or not. This method sets up a dual-task and assumes that patients have no difficulty remembering the content of the prime over short durations. Given the growing evidence that patients with neglect exhibit deficits in short term working memory (Husain and Rorden, 2003), the use of dual-task measures is problematic.

Other studies indicate that explicit detection on the neglected side need not necessarily reflect the level of implicit representation. For instance, Cohen et al. (1995) found that patients with neglect were not impaired in the perceptual processing of feature information presented to the neglected side, as contralesional...
flankers primed as well as those presented ipsilesionally. Rather, the authors showed that patients were impaired in the generation of an overt response, as they were slower to report the colour of a contralesional flanker compared to an ipsilesional flanker (Cohen et al., 1995). Similarly, several studies examining visual search or feature detection in patients with neglect have shown that stimulus presentation times to detect features in the contralesional field must be longer or precede the same feature in the ipsilesional field by several hundred milliseconds when an overt response is required (Rorden et al., 2004; Brooks et al., 2005). In the Brooks et al. (2005) study, feature search displays with 4 or 8 items were presented in an arc 7° from fixation in the right or left visual field (unilateral displays), or bilaterally with 8 or 16 items in a circular array around fixation (bilateral displays). The target was a green square presented in an array of red distractor squares (target was present on half the trials). Although accurate detection of feature targets on the contralesional side required longer stimulus durations than those presently ipsilesionally, increasing the number of distractors (whether in unilateral or bilateral displays) had no effect on performance. While these results suggest that feature encoding was delayed when feature displays were projected to the damaged hemisphere, an alternative explanation is that the strength of feature encoding was relatively normal in the damaged hemisphere, but the representation did not reach the threshold necessary for the generation of an overt response. In order to test these two alternatives we designed a study using similar feature displays to those used by Brooks et al. (2005) and examined both explicit feature detection and implicit feature priming. We also included conjunction search displays to explore explicit and implicit processing when conjoining of features was required.

To control for the level of explicit detection across features and conjunctions, and to measure the magnitude of influence of implicit representations, we conducted a two-part experiment with five patients with left hemispatial neglect (four in Experiment 1). For the first part we used a search array (feature or conjunction) and established display durations to distinguish two levels of difficulty (25 and 75% detection). Durations were determined psychophysically by adjusting the presentation time of the displays using a staircase procedure and an algorithm derived by Kaernbach (2001). In this way both feature and conjunction search displays were equated for difficulty of detection. For the implicit task we used the same search displays as primes. Participants could now ignore the flashing prime and were asked simply to make a speeded discrimination of a single probe stimulus presented at central fixation. The prime was presented at intervals pre-determined in the explicit detection task (25 and 75% accuracy threshold presentation times). Thus, the prime was more or less likely to be explicitly detected prior to the onset of the probe. The critical question was whether the probability of explicit detection would predict the priming results in the implicit task. If features and conjunctions are represented below the level of awareness but the capacity to generate an overt response is deficient, then priming could be similar whether the patient is more (75%) or less (25%) likely to explicitly detect the prime.

### Methods

#### Patient participants

Four of the five patients described below participated in Experiment 1 (R.L., B.W., D.S. and J.F.). Patient B.W. and an additional patient (D.W.), participated in Experiment 2. All patients were tested in the post-acute phase of injury (>3 months post-stroke) when they exhibited stable behavioural baselines. All patients exhibited mild to moderate symptoms of neglect on the Standard Comprehensive Assessment of Neglect, as detailed below (SCAN; McGlinchey-Berroth et al., 1996). All patients had normal or corrected to normal visual acuity, intact hearing, and performance within normal limits on the Mini Mental Status Exam. With the exception of B.W., all patients had full visual fields upon neurological exam.

R.L., a 57-year-old male suffered a large right middle cerebral artery (rMCA) infarct 8 months prior to testing (Fig. 1). His lesion included temporal, inferior parietal, temporal parietal junction, inferior frontal and subcortical (lenticular) areas in the right hemisphere. On the SCAN, he averaged 30% omission of all contralesional targets on line cancellation and search tasks, a 4mm average rightward misbisection on line bisection, and evidence of space-based neglect on a copy subtest (e.g. completely omitting one object on the left).

D.S., a 26-year-old male suffered an embolic stroke affecting the territory of the right middle cerebral artery 16 months prior to testing. The extent of his stroke included inferior parietal, temporal parietal junction, superior temporal and inferior/middle frontal areas in the right hemisphere. On the SCAN, he averaged 12% omission of all contralesional targets on cancellation and search tasks, a 4mm average misbisection on line bisection, and evidence of object-based neglect on a copy subtest.

J.F., a 74-year-old male suffered two successive right middle cerebral artery infarcts between 2002 and 2003 and at the time of testing continued to exhibit symptoms of neglect and extinction. His lesion included areas of the superior temporal gyrus, inferior parietal and posterior parts of the frontal lobe. On the SCAN, he averaged 20% omission of all contralesional items on cancellation and search tasks, had an average rightward deviation of 20mm on line bisection and visual and auditory extinction on confrontation testing.

B.W., a 64-year-old male suffered an embolic stroke during a surgical procedure in 2006. The infarct affected the inferior parietal lobe, superior temporal lobe and posterior parts of the frontal lobe. On the SCAN, he showed an average rightward deviation of 18mm on line bisection, missed 33% of left items on cancellation and search tasks and showed visual extinction on confrontation testing. He also showed a minor left, lower quadrantopia that did not affect his ability to see the entire search display used in the current study without having to move his eyes. B.W.’s field loss did not affect his ability to participate; in fact B.W. exhibited the fastest search speed compared to all other participants.

D.W., a 66-year-old male suffered a stroke in 2007 affecting the right middle cerebral artery. His stroke affected the inferior parietal and superior temporal lobe. On the SCAN, he missed 12% of left items on cancellation and search tasks, and showed an average rightward deviation of 11mm on line bisection.

#### Explicit task

To vary explicit detection rates while equating for detection difficulty, we varied stimulus presentation times to determine 75% and 25%
detection probability thresholds (easy versus hard) for both feature and conjunction search arrays for each patient individually. The explicit task was followed immediately by the implicit task.

In the explicit task patients were simply asked to report whether the target was present or absent (‘yes’ or ‘no’). Feature and conjunction search tasks were run in separate blocks. For conjunction search, the target (red triangle) was located among distractors sharing the same colour or shape (red squares and blue triangles). For feature search, the target (blue triangle) was located among distractors sharing the same colour (blue squares; Fig. 2 shows search displays used in explicit implicit tasks). Pilot testing revealed no differences attributable to target triangle colour. Targets randomly appeared in one of the eight locations to the left or right of fixation in a circular array, all within 4° of fixation. So that patients would focus attention on the relevant side of the display (i.e. to control for the influence of extinction), the target side was blocked. Patients were instructed to keep their eyes on a central fixation mark, and eye movements were monitored by the experimenter. Trials in which participants moved their eyes were excluded from analysis (average of four participants = 8%). Each trial began by the experimenter pressing a key on an external keyboard when the patient’s eyes were focused on central fixation.

The stimuli were presented on a laptop computer screen located 60 cm in front of the patient. Presentation duration of the visual stimulus array was adjusted according to the participant’s performance via a psychophysical staircase procedure that controls for response bias (Kaernbach, 2000). Presentation time was fit to a 75% and 25% target detection threshold. Presentation time began at 2000 ms and was adjusted in increments of $\Delta T = 6 \times \left(\left\lfloor \left(\left\lfloor \frac{r + 1}{2} \right\rfloor \right) \right\rfloor \times 16 ms$), where $r$ = the number of reversals encountered and mod (a, b) is the remainder after division of a by b. Detection thresholds for each condition were based on the last 8 of 10 reversals in the staircase for each condition. Staircases for 25% and 75% detection were interleaved and attention was controlled by beginning the next trial only when the participant indicated they were ready. Using this procedure, estimates of threshold presentation time (TPT) for

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**Figure 1** Flair and $T_1$-weighted magnetic resonance images (MRI) of patient participants. Selected axial slices show extent of right hemisphere lesion. Arrow indicates site of lesion for participant D.S. (see Methods section for detailed description).
target detection could be established in a relatively short period of time (5–7 min).

**Implicit task**

Search displays used in the explicit task were presented as primes on each trial at either the 75% threshold presentation time (high detection probability condition) or 25% TPT (low detection probability condition), unique to each participant. These intervals were chosen because we could be assured that features or conjunctions were encoded on some proportion of the trials at each display time, but that explicit detection would happen on fewer trials in the 25% than 75% TPT condition. High and low TPT primes were randomly presented with the provision that half the trials were high and half low. Feature and conjunction conditions were run separately. Participants were told they only had to respond to a central probe item that appeared 500 ms after the offset of the search display (prime) and to ignore the peripherally presented displays. The patients were asked to respond as quickly and accurately as possible ('yes' response to a target probe, or 'no' response to an orange circle; Fig. 2). The probe remained on the screen until the patient made a response (collected via voice onset recording equipment) and reaction time (RT) and discrimination accuracy were recorded.

To control for differences in prime duration, an index of the priming effect was calculated for each condition: conjunction, high and low detection; feature, high and low detection. The priming effect was determined by subtracting the mean reaction time for correct responses to the target probe following either the feature or conjunction prime from the mean reaction time for trials in which the target probe was preceded by a neutral prime presented for the same durations (both high and low TPTs; see Fig. 2). The neutral feature prime and neutral conjunction prime consisted of all the objects in the feature prime (blue squares) or all the features/conjunctions in the conjunction prime (blue triangles, red squares), except the critical item (red triangle in feature prime). Thus, the priming effect index reflected only the influence of the relevant target item and not the related distractors. The neutral display was presented on 50% of trials and the order of presentation was randomized.

Each participant completed six test sessions; each session consisted of one practice block of 48 trials and four test blocks of 96 trials each. Order of blocks was counterbalanced as follows: feature, conjunction, feature, conjunction in sessions 1, 3 and 5, and conjunction, feature, conjunction, feature in sessions 2, 4, and 6.

**Experiment 1**

**Results**

**Explicit task**

All patients exhibited a ceiling effect for targets located to the right of fixation (i.e. no reliable difference between high and low detection threshold presentation times in both the conjunction and feature search conditions, $P's > 0.05$). Thus, only contralateral target displays were evaluated in Experiment 1. Each participant’s outcome was considered individually: ANOVAs on mean threshold presentation times with Detection-Level (75, 25) and Search-Type (Feature, Conjunction) as factors revealed significant main effects of Detection-Level and Search-Type ($P's < 0.001$) for each participant and a significant interaction between Detection-Level and Search-Type [R.L.: $F(1,20) = 98.863$, $P < 0.001$; J.F.: $F(1,20) = 33.145$, $P < 0.001$; D.S.: $F(1,20) = 25.095$, $P < 0.001$; B.W.: $F(1,20) = 124.322$, $P < 0.001$]. Planned comparisons revealed that mean threshold presentation times to produce equal detection difficulty at 75% were significantly faster for feature than conjunction search for all participants [R.L.: 208 ms versus 1092 ms, $t(1) = -10.109$].
Table 1 Mean TPT in milliseconds by condition for each participant in Experiment 1

<table>
<thead>
<tr>
<th>Left prime: high contrast</th>
<th>25% aware condition</th>
<th>75% aware condition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Feature (ms)</td>
<td>Conjunction (ms)</td>
</tr>
<tr>
<td>R.L.</td>
<td>24</td>
<td>36 (P = 0.056)</td>
</tr>
<tr>
<td>J.F.</td>
<td>88</td>
<td>102 (ns)</td>
</tr>
<tr>
<td>D.S.</td>
<td>176</td>
<td>408*</td>
</tr>
<tr>
<td>B.W.</td>
<td>28</td>
<td>24 (ms)</td>
</tr>
</tbody>
</table>

A ‘*’ indicates significance (P < 0.05).
ns: not significant

P < 0.001; J.F.: 396 ms versus 896 ms, t(1) = -6.731, P < 0.003; D.S.: 488 ms versus 1590 ms, t(1) = -7.945, P < 0.0001; B.W.: 72 ms versus 150 ms, t(1) = -14.315, P < 0.0001; see Table 1. Threshold presentation times to produce equal detection difficulty at 25% were as follows: D.S. demonstrated significantly faster feature search [176 ms versus 408 ms, t(1) = -3.057, P < 0.01], R.L. showed a non-significant trend in the same direction [24 ms versus 36 ms, t(1) = -2.157, P < 0.056] and J.F. and B.W. did not exhibit a significant effect of search type at low probability of detection [J.F.: 88 ms versus 102 ms, t(1) = -0.969, P > 0.387; B.W.: 28 ms versus 24 ms, t(1) = 0.777, P > 0.455].

Overall, three of four subjects exhibited the expected direction in the low-awareness condition (i.e. conjunction search longer than feature search). Although this would justify a one-tailed test, nevertheless, we used the more stringent two tailed test which resulted in a significant difference only for D.S. when averaging the last eight reversals (note that R.L.’s difference was nearly significant, P = 0.056). Because of the difficulty of the low awareness condition, patients differed in terms of how quickly their data became stable. J.F.’s performance was highly variable, and thus differences between conjunction and feature target detection in the 25% condition were not significant despite the fact that mean conjunction TPT was longer than mean feature TPT. As in prior studies (see List et al., 2008) when we averaged his last four reversals we found a significant difference in TPT with mean feature detection duration significantly shorter (38 ms) than conjunction detection [98 ms, t(46) = 1.66, P < 0.05]. This difference is likely a more accurate representation of his TPT as his performance was stable and the distribution of reversal values flat. B.W. was the highest functioning patient; accordingly, his threshold presentation times in the 25% condition were close to the refresh rate of the screen (16 ms), and thus differences that may have actually existed were likely obscured due to technical limitations.

**Implicit task**

Figure 3 shows priming effects (mean reaction time to probe preceded by either feature or conjunction prime—mean reaction time to probe preceded by the related neutral prime presented at the same TPT). Priming effects for feature and conjunction conditions for each patient are shown (Table 2). The only difference between the two conditions was whether a feature or conjunction prime preceded the probe and how long the prime appeared (as estimated by the explicit task).

An ANOVA with Detection-Level (25 and 75%) and Prime-Type (Feature, Conjunction) as factors revealed significant main effects of Detection-Level and Prime-Type (P's < 0.05) on priming and a significant interaction between Detection-Level and Prime-Type for R.L. [F(3,20) = 4.01, P < 0.05], J.F. [F(3,20) = 6.294, P < 0.02], B.W. [F(3,20) = 7.56, P < 0.01] and D.S. [F(3,20) = 5.44, P < 0.03]. Planned comparisons showed that mean feature priming was not dependent on Detection-Level for any patient; feature displays did prime, but the effect did not differ between high and low probability detection levels, respectively: R.L., −35 ms versus −41 ms [(t(1) = −0.25, P = 0.80)]; J.F., −27 ms versus −19 ms [(t(1) = 1.10, P = 0.297)]; B.W., −28 ms versus −25 ms [(t(1) = −0.315, P = 0.75)]; D.S., −30 ms versus −26 ms [(t(1) = −0.35, P = 0.73)]. Conversely, for conjunction primes, high detection levels produced significantly greater priming compared to low detection levels: R.L., −39 ms versus 7 ms [(t(1) = −2.22, P < 0.05)]; J.F., −47 ms versus 17 ms [(t(1) = −2.285, P < 0.04)]; B.W., −38 ms versus 11 ms [(t(1) = −3.676, P < 0.01)]; D.S., −62 ms versus −16 ms [(t(1) = −2.71, P < 0.02)].

**Discussion**

The results of the explicit task are consistent with previous findings in that less time was needed to respond correctly to a feature than a conjunction. We also replicated previous results showing that feature target detection on the contralesional side improves with duration (Brooks et al., 2005). However, in the implicit task in which no overt response to the prime was necessary, we showed that features prime equally well whether they were more or less likely to be explicitly detected (i.e. no difference in the priming effect between low and high feature prime conditions). This pattern of results was present for all patients and demonstrates that features projected to the damaged hemisphere are represented early and separately from the overt response. Conversely, in all patients conjunction priming was larger when targets were more likely to be explicitly detected (high TPT condition) than when they were less likely to be detected (low TPT condition). Because the priming effect was calculated by comparing reaction time to the conjunction prime versus reaction time to a neutral prime comprised of the same configuration of features as the conjunction prime but without the critical item (i.e. target item or red triangle), a priming effect can only be attributed to the presence of the relevant target item and not related features.

To determine whether the differences in feature versus conjunction priming in Experiment 1 were the result of damage to the attention system, we examined processing within and between each hemifield. Because we were unable to reliably elicit a difference in search thresholds between high and low probability conditions when targets were presented ipsilaterally in Experiment 1 (ceiling effect), we utilized the same experimental design, but lowered the contrast of the search displays making detection more difficult. This enabled us to reliably estimate differences in explicit detection for targets presented to the left or right of fixation, and assess the impact of damage to the dorsal system on explicit detection and implicit representation.
To directly examine the effect of dorsal damage on explicit and implicit feature and conjunction processing, we conducted a second experiment using the same design and search displays as Experiment 1 but reduced the contrast by 90%. When we lowered the contrast, however, patient participants R.L., J.F. and D.S. were unable to reliably detect low-contrast targets in the explicit task. Thus, patient B.W., and another patient participant (D.W.), capable of reliably detecting low-contrast targets presented to either the ipsilesional or contralesional side of space, were evaluated in Experiment 2. Also, despite the reduced contrast, six age-matched controls (mean age = 56) run under the same conditions failed to show reliable differences between high and low probability conditions, particularly for feature search due to a ceiling effect (displays were too easy). Because

![Figure 3](https://academic.oup.com/brain/article-abstract/132/7/1889/326101)

**Figure 3** The priming effect per condition (feature or conjunction prime/high TPT or low TPT) in Experiment 1: RT to relevant probe presented at central fixation when preceded by a conjunction or feature prime minus when it was preceded by a neutral conjunction or feature display. Results show that there was no significant effect of attention on magnitude of feature priming whereas in the conjunction prime condition, only primes presented at the high TPT duration produced a significant priming effect compared with the low TPT condition.

**Table 2** Mean RT by prime type for each participant in Experiment 1

<table>
<thead>
<tr>
<th>Left prime: high contrast</th>
<th>25% aware condition</th>
<th>75% aware condition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Feature – neutral = effect (ms)</td>
<td>Conjunction – neutral = effect (ms)</td>
</tr>
<tr>
<td>D.S.</td>
<td>764 – 794 = −26</td>
<td>832 – 848 = −16</td>
</tr>
</tbody>
</table>

Priming effect (‘Effect’) = RT to correctly respond to a centrally presented probe preceded by either a feature or conjunction display presented at either low (25%) or high (75%) probability of detection minus a neutral feature or conjunction prime presented at the same duration.

**Experiment 2**

To directly examine the effect of dorsal damage on explicit and implicit feature and conjunction processing, we conducted a second experiment using the same design and search displays as Experiment 1 but reduced the contrast by 90%. When we lowered the contrast, however, patient participants R.L., J.F. and D.S. were unable to reliably detect low-contrast targets in the explicit task. Thus, patient B.W., and another patient participant (D.W.), capable of reliably detecting low-contrast targets presented to either the ipsilesional or contralesional side of space, were evaluated in Experiment 2. Also, despite the reduced contrast, six age-matched controls (mean age = 56) run under the same conditions failed to show reliable differences between high and low probability conditions, particularly for feature search due to a ceiling effect (displays were too easy). Because
feature detection is so rapid under normal circumstances, technical limitations related to the refresh rate of the computer screen (16 ms) prohibited evaluation of normal controls using the same stimulus parameters as those used with patient participants.

Results

Explicit task
As in Experiment 1, a 75% and 25% TPT was acquired (see Implicit task Experiment 1 above) for both feature and conjunction targets presented either to the left or right of fixation (blocked). Both patients exhibited reliable threshold presentation times for low and high detection conditions for left and right target. ANOVAs on mean threshold presentation times with Detection-Level (75 and 25%), Search-Type (Feature, Conjunction) and Target Side (left, right) as factors revealed significant main effects of Detection-Level, Search-Type and Target Side (P’s < 0.001) for each participant and significant two-way interactions between Detection-Level and Search-Type [B.W.: F(1,40) = 22.875, P < 0.001; D.W.: F(1,40) = 140.851, P < 0.001] and Detection-Level and Side [B.W.: F(1,40) = 203.859, P < 0.001; D.W.: F(1,40) = 168.478, P < 0.001]. Planned comparisons revealed that mean threshold presentation times to produce equal detection difficulty at 75% were significantly faster for feature than conjunction search for both participants regardless of side (P’s < 0.05). For 25% detection probability, D.W.’s feature was significantly faster than conjunction across side [45 ms versus 152 ms, t(22) = -3.171, P < 0.01] whereas B.W. did not show a difference between feature and conjunction displays at low probability of detection [28 ms versus 34 ms, t(22) = -1.315, P = 0.202].

Implicit task
Figure 4 shows priming effects (mean reaction time to probe preceded by either feature or conjunction prime—mean reaction time to probe preceded by the related neutral prime presented at the same threshold presentation times; also see Table 3). Priming effects for feature and conjunction conditions for each patient are shown for each target side.

An ANOVA with Detection-Level (25 and 75%), Prime-Type (Feature, Conjunction) and Side (left, right) as factors was run individually to evaluate each patient’s priming data. Importantly, B.W. and D.W. showed a significant two-way interaction between Detection-Level & Prime-Type (P’s < 0.01) that did not differ

![Figure 4](https://academic.oup.com/brain/article-abstract/132/7/1889/326101)
by side. Planned comparisons showed that detection level produced no difference in priming for features for either patient on either side (P's > 0.05). However, differences in priming for conjunctions reflected differences in probability of detection, with higher probability of detection resulting in greater priming: B.W., −2 ms versus −32 ms, t(22) = −5.425, P < 0.001; D.W., 15 ms versus −32 ms, t(22) = 7.776, P < 0.001.

Although there were no interactions with Side for B.W., there was a larger difference in mean priming for D.W. on the right versus the left in the high detection probability conjunction condition resulting in significant Detection-Level × Side [F(1,40) = 5.813, P < 0.05] and Prime-Type × Side [F(1,40) = 10.100, P < 0.01] interactions. The overall analysis also revealed a main effect of Detection-Level for both patients (P's < 0.01).

### Discussion

The results of Experiment 2 are consistent with Experiment 1 and demonstrate that in the implicit task, features prime equally well whether they are more or less likely to be detected when an overt response is necessary (i.e. no difference in the priming effect between low and high feature prime conditions). This pattern was present for both patients and demonstrates that features projected to either hemisphere are represented early. Damage to the attention system does not appear to influence implicit feature encoding, as features that are less likely to enable the generation of an overt response (25% condition) are still capable of priming to the same degree as those that are more likely to enable response. Conversely, in both patients conjunction priming was larger when targets were more likely to be explicitly detected (high TPT condition) than when they were less likely to be detected (low TPT condition) regardless of side of presentation. For patient D.W., the relative difference in the conjunction priming effect (low TPT versus high TPT) was greater when the prime was projected to the intact or left hemisphere. This effect was evident despite longer threshold presentation times for left hemifield primes than right hemifield primes. B.W. did not show a difference in the magnitude of conjunction priming between hemispheres. The greater relative difference in conjunction priming (75% versus 25%; right visual field > left visual field) in one patient suggests that the intact field may enable greater implicit representation.

However, while damage to the attention system may negatively affect the relative strength of the conjunction representation, it is clear that the greater the probability for overt detection the greater the strength of the conjunction representation regardless of location.

Growing evidence confirms the notion that features are processed in the neglected field whether or not they are detected (Riddoch and Humphreys, 1987; Eglin et al., 1989, 1994; Cohen et al., 1995; Esterman, et al., 2000; Laeng et al., 2002; Pavlovskya et al., 2002; Robertson et al., 2003; Brooks et al., 2005). Many of the same studies indicate that unilateral or bilateral parietal lobe damage and the concomitant loss of spatial awareness is accompanied by deficits in discriminating targets that require the integration of two or more features. Theoretically, this difference in processing features versus conjunctions, particularly in search paradigms, has been attributed to qualitatively different processes. For instance, Feature Integration Theory (FIT) proposed that conjunction search requires a serial deployment of attention due to the requirement that feature must be bound, while feature search can be performed in parallel (Treisman and Gelade, 1980). Biased Competition Theory (BCT), an influential alternative to Feature Integration Theory, proposes that since conjunctions are typically less salient than simple features, there is more competition between distractors and the target when searching for a conjunction, and consequently, longer search durations in conjunction search compared with feature search (Desimone and Duncan, 1995).

Still others propose that serial conjunction search is guided by parallel pre-attentive processes (Guided Search: Wolfe et al., 1989). The findings in patients with spatial deficits have been interpreted as supporting each of these accounts by different investigators. However, the results of the current study clearly indicate an important role of spatial attention in overtly searching for conjunctions compared to features. Because prime durations were fit to pre-determined levels of overt response threshold (high versus low), unique to each patient, it is difficult to argue that the present effects are simply the result of longer presentation times. Rather, conjunction primes that were more likely to be overtly detected produced stronger priming effects than those that were less likely to be overtly detected, while feature primes were influential independent of overt detection rates.

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### Table 3 Mean RT by prime type for each participant in Experiment 2

<table>
<thead>
<tr>
<th>Low-contrast</th>
<th>25% aware condition</th>
<th>Conjunction – neutral = effect (ms)</th>
<th>75% aware condition</th>
<th>Conjunction – neutral = effect (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left prime</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Right prime</td>
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Primings effect (‘Effect’) = RT to correctly respond to a centrally presented probe preceded by either a feature or conjunction display presented at either low (25%) or high (75%) probability of detection minus a neutral feature or conjunction prime presented at the same duration.
The fact that features prime equally well whether they are more or less likely to be explicitly detected suggests that latency differences between contra- and ipsilesional feature target detection in prior studies are likely due to a post-perceptual process (Riddoch and Humphreys, 1987; Eglin et al., 1989, 1994; Esterman et al., 2000; Laeng et al., 2002; Pavlovskaya et al., 2002; Robertson et al., 2003; Robertson and Brooks, 2006). Because search or detection measures rely on access by consciousness to an overt response, the nature of the representation before the generation of response has been indeterminable (e.g. Rorden et al., 2004; Brooks et al., 2005). However, the findings from Cohen et al. (1995) suggest that latency differences may be due to delay in the generation of an overt response, a relatively late process. Using a flanker task, the authors showed that patients with neglect were capable of generating appropriate response codes. Central targets benefited from congruent contralesional or ipsilesional flankers equivalently. However, when patients were required to explicitly report the colour of the contralesional target, significant delays were evident. The authors did not, however, examine the influence of conjunction flankers only simple features (e.g. colour). A study in normal, healthy perceivers has examined the effect of conjunction flankers (Lavie, 1997) and showed that attention to the flanker resulted in larger effects from conjoined features than when the flanker was not attended. These results support the findings from the current study suggesting a distinction between the implicit representations of features and conjunctions.

The current results are also consistent with neurobiological models that suggest that encoding of features occurs in parallel and relies on feedback connections, while conscious selection is influenced more by feedback connections to earlier areas (e.g. Hochstein and Ashihar, 2002). Although our data are consistent with such models, at this point the relationship is unclear. Additional studies are needed to determine the degree to which priming effects are related to the level of pre-attentive encoding versus access to fully encoded representations and the neurobiological mechanisms that support them.

In summary, the current study reports the effects of feature and conjunction priming in five patients with hemispatial neglect and shows that when two features must be conjoined, the magnitude of explicit detection predicts the strength of the implicit representation. Consistent with prior studies, the current study also shows that the effects of feature priming appear unaffected by level of awareness.

References


