

Implicit Representations of Space after Bilateral Parietal Lobe Damage

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Abstract

■ There is substantial evidence that the primate cortex is grossly divided into two functional streams, an occipital–parietal–frontal pathway that processes “where” and an occipital–temporal–frontal pathway that processes “what” (Ungerleider and Mishkin, 1982). In humans, bilateral occipital–parietal damage results in severe spatial deficits and a neuropsychological disorder known as Balint’s syndrome in which a single object can be perceived (simultanagnosia) but

its location is unknown (Balint, 1995). The data reported here demonstrate that spatial information for visual features that cannot be explicitly located is represented normally below the level of spatial awareness even with large occipital–parietal lesions. They also demonstrate that parietal damage does not affect preattentive spatial coding of feature locations or complex spatial relationships between parts of a stimulus despite explicit spatial deficits and simultanagnosia. ■

INTRODUCTION

It would be hard to underestimate the impact of Ungerleider and Mishkin’s 1982 article in which they proposed two cortical visual streams of processing. The animal and human literature converged to suggest a dorsal stream for processing space (the “where” pathway) and a ventral stream for processing objects (the “what” pathway). Refinements have been made but the experimental support for their original thesis is now extensive.

Consistently, neuropsychological data have shown that occipital–temporal damage in humans can produce agnosias for features and objects (Farah, 1990) whereas parietal lobe damage results in deficits of spatial orientation (De Renzi, 1986), spatial attention (Posner, Walker, Friedrich, & Rafal, 1984), and spatial awareness (Bisiach, Capitani, Luzzatti, & Perani, 1981). Spatial functions of the parietal lobe have taken on added importance in light of recent reports that damage to both parietal lobes disrupts the ability to correctly bind features (e.g., color, shape, size, motion) even under free viewing conditions (Humphreys, Caterina, Wolfe, Olson, & Klempen, 2000; Bernstein & Robertson, 1998; Robertson, Treisman, Friedman-Hill, & Grobovecky, 1997; Friedman-Hill, Robertson, & Treisman, 1995). This binding problem makes it very difficult to accurately search a cluttered array for the conjunction of two features (e.g., red X among red O and green X distractors), although detecting features remains relatively in-

tact. However, detecting a feature’s location may be nearly impossible. These results were predicted by “feature integration theory,” which proposed that attention to a *spatial* location is necessary for proper feature binding but *spatial* attention is not necessary to detect their presence (Treisman & Gelade, 1980; Treisman & Schmidt, 1982). The binding deficits in patients with parietal damage strongly suggest that spatial functions of the parietal lobe interact with features coded in ventral areas (e.g., color, shape, size, etc.) to solve the binding problem (Treisman, 1998; Robertson et al., 1997).

Some investigators have argued that posterior portions of the ventral stream have adequate spatial resolution to support feature binding (Desimone & Duncan, 1995). The major evidence to support this conclusion was from single-unit recording data in monkeys. However, the previously discussed observations in patients with bilateral parietal lesions demonstrate that intact temporal lobes are not sufficient to support normal perception of correctly bound features, the correct localization of separate features or the perception of more than one object at a time. Nevertheless, the implicit coding of feature locations may occur. It would seem that some type of spatial information must remain intact to support the spatial configurations that define single objects or shapes that are explicitly or implicitly perceived.

Robertson et al. (1997) were the first to report preliminary evidence to support the hypothesis that spatial information that cannot be accessed explicitly remains below the level of awareness in a patient with bilateral occipital–parietal damage resulting in Balint’s syndrome (R.M.). R.M. was slower to read the word “up” or “down” when it was presented in an incon-

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sistent location to its meaning in a rectangle than when it was presented in a consistent location. On the other hand, his ability to locate the words was at chance. The present studies are designed to determine whether the location of and spatial relationships between individual features are represented below the level of awareness. If so, this would suggest that multiple features are spatially represented without parietal involvement but that the parietal lobe is necessary to explicitly perceive their locations.

Balint's syndrome is fortunately quite rare, as it renders a person functionally blind in its classical form (Rafal, 1997; Holmes & Horrax, 1919; Balint, 1995). These patients can see only one object at a time (i.e., simultanagnosia), which may be either complex, simple, large, or small, but they cannot verbally report its location nor can they correctly point to or reach for the object they see. They report not knowing where it is, and there is no consistency in their location responses when they are forced to make a location judgment. This occurs despite intact primary motor and sensory visual abilities. These problems disrupt activities of everyday life as would be expected, and the patients themselves often report being blind. Language, memory, and other cognitive abilities remain relatively intact (Baylis, Driver, Baylis, & Rafal, 1994).

R.M. presented with classic Balint's syndrome in 1992. At age 54, he suffered sequential embolic infarcts a few months apart. MRI after his second stroke revealed large bilateral lesions in the angular gyrus (area 39), dorso-lateral occipital gyrus (area 19), and posterior dorso-lateral parietal lobes (portions of area 7). All medial areas were anatomically intact, as were temporal, frontal, and ventral occipital lobes, the supramarginal gyrus, postcentral gyrus, as well as subcortical structures. Primary visual cortex was unaffected. Visual acuity, contrast sensitivity, visual fields, and color vision were normal. Motor abilities were normal and spatial information regarding his own body was normal, demonstrating that his deficits were not due to spatial confusion (3-D MRI reconstruction of R.M.'s brain and detailed descriptions of R.M.'s visual abilities have been reported elsewhere (Robertson et al., 1997; Robertson, 1998; Robertson & Rafal, 2000; Friedman-Hill et al., 1995). The following experiments demonstrate that despite severe spatial attention deficits and simultanagnosia, the location of a single feature was recorded as well as its relationship to other features in the display. There are enriched spatial maps that are represented below the level of awareness when both parietal lobes are damaged that are capable of encoding complex displays containing multiple items.

EXPERIMENT 1

In the first study an indirect measure was used to test whether a feature's location was encoded implicitly.

Importantly, no spatial information was required to perform the task, as R.M. could not have done so.

A dual task was used in which a four-item search display was presented for 60 msec in a square-like configuration around a central fixation point. This display was followed by a probe in the middle of the screen at fixation (Figure 1). The search display contained one green (or red) circle and three red (or green) distractors. After the search display disappeared the fixation point changed to either an arrow or symmetrical form 60 or 300 msec later. Instructions were to respond as rapidly as possible by pressing the mouse key as soon as an arrow appeared and to withhold response if any other pattern appeared. It was not important which way the arrow pointed, only that an arrow was present. After this response was made, the task was to report whether a search target had appeared or not in the prior search display. The main dependent measures were the speed that subjects detected the arrow analyzed as a function of whether it pointed to where a target or distractor had appeared (although its orientation was not task relevant) and the error rate in reporting the presence or absence of a search target in the search display.

Results

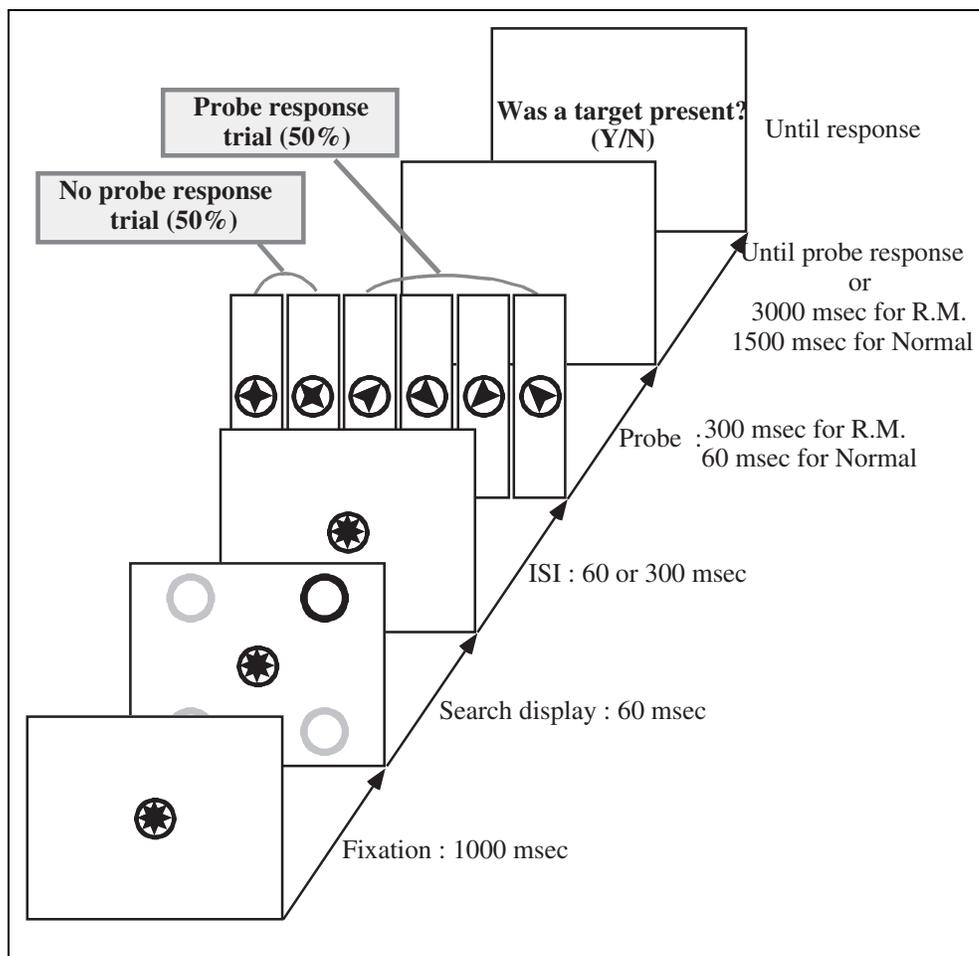
Normal Participants

Normal participants responded faster when the probe arrow pointed to the search target's prior location than to one of the distractor locations (Figure 2) even though neither the direction of the arrow nor the location of the search item was necessary to perform either task. Accuracy was good both for reporting the search target (98%) and for discriminating the arrow probe (99%) and only correct responses were included when calculating the mean reaction time (RT) for each cell of the design.

RTs to detect the arrow were analyzed with analysis of variance techniques (ANOVA) for repeated measures with spatial compatibility between the direction of the arrow probe and target location (target, target $\pm 90^\circ$, and target $+ 180^\circ$) and stimulus onset asynchrony (SOA—120 and 360 msec) as factors. Unsurprisingly, responses were slower in the short SOA condition than in long SOA condition [$F(1,12) = 12.7, p < .01$]. More importantly, there was a main effect of spatial compatibility [$F(2,24) = 4.9, p < .02$] but no interaction between SOA and spatial compatibility [$F < 1$].

Probe responses were faster when the arrow pointed to the feature target location than when it pointed to one of the distractor locations at both short and long SOAs, and RTs increased linearly over spatial compatibility (linear contrast for spatial compatibility: $F(1,12) = 8.5, p < .01$). Discrimination of the arrow was sensitive to the location of the target feature and the spatial

Figure 1. Example of a trial in the probe task. The dark circle in the search display represents the feature target and the light circles represent the distractors. One of the six probe patterns shown appeared in the middle of the screen by offsetting selected pixels of the fixation pattern. The first task was to press the mouse key as rapidly as possible whenever an arrow appeared and withhold response when one of the two other probes appeared. The second task was to vocally report the presence or absence of the feature target in the search display. Neither the arrow probe task nor the feature target detection task required a spatial response.



relationship between the target and distractors. Although neither the orientation of the arrow nor the location of the search target were necessary to perform the task, it is clear that the search display affected probe

performance at both short and long SOAs. The pattern is consistent with a type of spatial or attentional gradient that seems to have been automatically formed by the search target's location. The system remained sensitive to this gradient and affected probe detection time even when the search display disappeared.

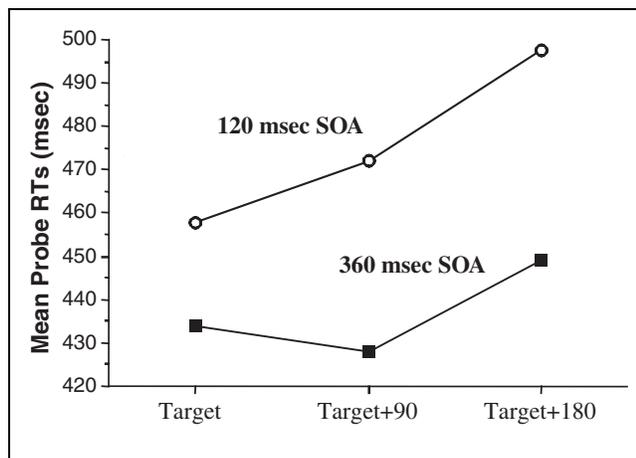


Figure 2. Performance in the probe task for normals. Mean RT to detect an arrow probe as a function of the spatial compatibility between the arrow's direction and the previously presented search target's location for normal participants.

Balint's Patient

R.M. was tested in the same paradigm. In order to obtain enough power for a single subject analysis, R.M. was run through eight sessions of the experiment with the search display containing a green target and red distractors. A mean was calculated for each cell of the design for each session. RTs were analyzed with sessions as the random factor and spatial compatibility and SOA as repeated measures. Detecting the arrow probe was good (93% accurate), and only correct trials were included in the RT analysis.

Like normals, this analysis revealed a significant main effect of SOA [$F(1,7) = 33.6, p < .01$] and of spatial compatibility [$F(2,14) = 9.3, p < .01$] and no interaction. Also like normals, R.M. responded more slowly at short SOAs than long and more quickly when the arrow probe pointed to the search target's prior location than

to the location of a distractor (Figure 3). RT increased linearly over spatial compatibility (linear contrast for spatial compatibility: $F(1,7) = 16.8, p < .01$).

To explore the spatial compatibility effects further, R.M. was run through another eight sessions in the same design but with a red search target and green distractors in an attempt to make the target more salient. His false alarms dropped to 1% with a hit rate of 27%. Although hits did not increase, false alarms were reduced by the increased salience, again showing that features were detected accurately on several trials (although as shown below their locations were not known). More important, RTs to the arrow probe did not change (target, 728 msec; target \pm 90, 767 msec; target + 180, 789 msec) except for an overall 127-msec faster response. As before there was a main effect of SOA and of spatial compatibility (both $p < .01$) but no interaction.

Unlike normals, R.M. was poor at reporting the feature search target in this design (28% hits and 15% false alarms). His hits were larger than false alarms [$\chi^2 = 12.81, p < .001$] indicating he did detect the target accurately on some occasions. The next section demonstrates that this was due to the dual task procedure.

Dual task control condition. A subsequent procedure demonstrated that R.M.'s poor feature detection performance was due to either the extra attentional demands of a dual task or to the added memory load. When the arrow probe task was eliminated and only the search display was presented for 60 msec in a block of 40 trials, he missed the target on three trials. As expected, he was unable to report its location (13%) when he detected its presence and on nearly half the trials reported it as in the center even though he was in-

structed to make a four-alternative choice response (upper right or left, lower right or left).

Although R.M.'s responses to detect the arrow were slower than normals in the main probe experiment, his speed to discriminate the arrow was sensitive to the location of items in the prior search display. This occurred despite the difficulty he had when asked to locate the search target when the search display was presented in isolation. This difficulty was also seen in the quality of his responses. He had to be pushed to guess the locations and often shook his head back and forth in clear frustration.

Explicit spatial attention control condition. It remained possible that the additional spatial information provided by the arrow in the main experiment helped R.M. to explicitly recall the spatial relationship between the arrow's orientation and the location of the feature search target. For this reason an additional experiment examined R.M.'s explicit spatial abilities with these types of displays. The strongest test of R.M.'s ability to perceive these spatial relationships could be tested by showing the search display and the central arrow in free view for as long as he needed to make an explicit spatial judgment. To do this, the search displays were presented simultaneously with the central arrow (Figure 4) and remained on the screen until he responded. The arrow either pointed to the target or one of the distractors, and he was asked to report "yes" if the arrow pointed to the target and "no" if it did not. Given his spatial deficits, we expected him to have difficulty with this task.

The stimuli were the same as those in the main experiment except that the search display and the central arrow appeared at the same time. There were no target-absent trials. The target was always present at one of four locations that was randomly selected on each trial with the constraint that it appeared equally often in each location. The task was to verbally report whether the arrow pointed toward the target or not. There were 48 trials. On half the trials the arrow pointed to the target and on the other half it pointed to one of the distractors.

R.M. could not determine the spatial relationship between the arrow and the feature target (Figure 4). His yes responses were similar whether the arrow pointed to a target or distractor (62.5% and 61%, respectively). Again, he reported this to be a difficult task, shook his head side to side, and took more than 20 sec on average to respond to each display.

It should be noted that his problems were not due to spatial confusions per se. He had full spatial awareness of the location of his own body parts and the spatial relationships between them even when his Balint's symptoms in everyday life were more severe than at the time of this study (Robertson et al., 1997). He could correctly report the location of a touch to his back or arms, raise his right or left hand on command, and was

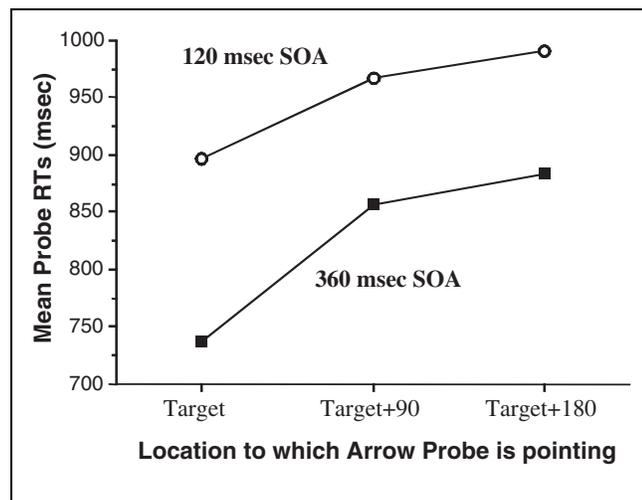
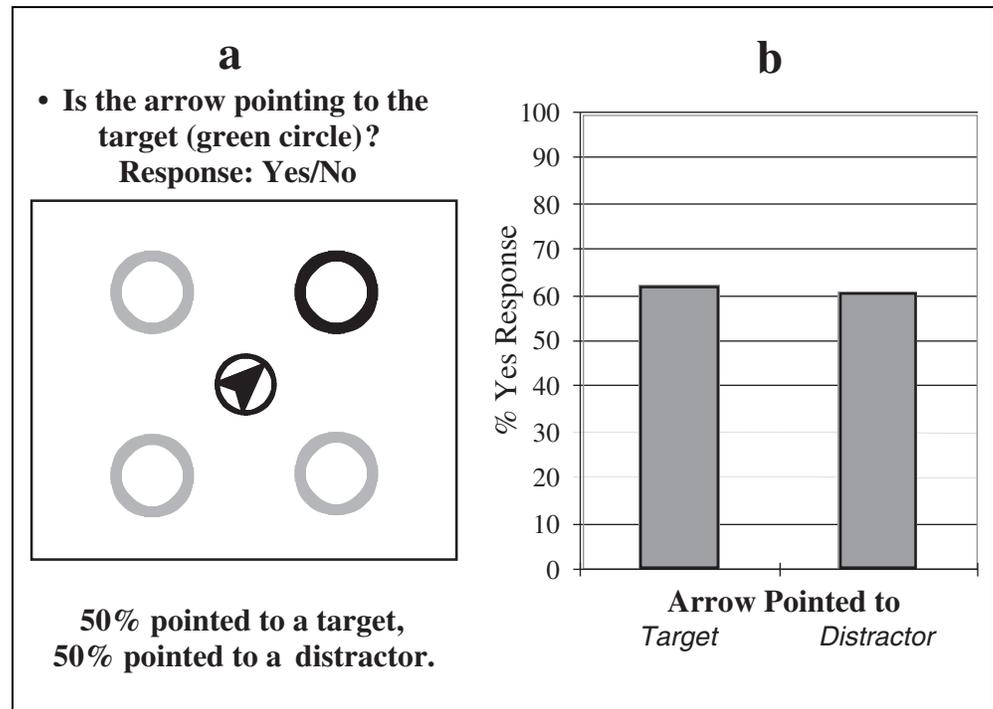


Figure 3. Performance in the probe task for R.M. Mean RT to detect an arrow probe as a function of the spatial compatibility between the arrow's direction and the previously presented search target's location for patient R.M.

Figure 4. (a) Example of a stimulus presented without time limits to R.M. in the explicit spatial attentional control condition; (b) the proportion of yes responses when the arrow pointed toward a target versus distractor.



always capable of following instructions such as “grab your left ear with your right hand.”

EXPERIMENT 2

In a second visual search experiment we confirmed that conjunction search continued to be difficult for R.M. whereas feature search was relatively easy as reported previously (Robertson et al., 1997). Search displays were presented on each trial and consisted of eight colored items arranged in a circle around a central fixation point. R.M. was asked to report the presence or absence of a red circle among green distractors in feature search and a red X among red Os and green Xs in conjunction search. It was emphasized that he should only respond when he was confident that the target was present. (An attempt to perform the dual task with the arrow probe using four-item conjunction displays proved too difficult for R.M. and that experiment was abandoned.) By testing feature and conjunction search at the same time, we could address the issue of whether the implicit spatial representation that supported the spatial compatibility effects in Experiment 1 could support conjunction search. If not, then it would demonstrate that this spatial representation is not sufficient to support binding.

Results

Feature search was relatively good (83% hits and 1% false alarms), whereas conjunction search was poor

(31% hits and 20% false alarms). The false alarm rate in conjunction search is consistent with R.M.’s previously reported illusory conjunctions. If red is inappropriately bound to one of the green Xs in target-absent displays, then a red X is perceived and a yes response would follow. These results are also consistent with R.M.’s previously reported search performance and feature binding errors and supports the idea that feature binding requires explicit spatial awareness (Robertson et al., 1997).

DISCUSSION

Together the results from these experiments demonstrate that bilateral parietal damage produces chronic deficits in explicitly perceiving spatial relationships even under free viewing conditions but that complex spatial relations continue to influence performance. Despite the fact that R.M. could not report the location of a feature target above chance level nor discriminate whether an arrow pointed to the target, the pattern of his RT performance when detecting the centrally presented arrow probe was similar to normal participants. Kim and Cave (1995, 1999) previously showed that for normal college students a dot probe appearing after a feature display similar to that used here was detected faster if it was presented at the target location than if it was presented at the location of a distractor. They argued that spatial attention was automatically drawn to the location of a unique feature during its brief presentation, producing faster RTs when a dot appeared at the same location a few

milliseconds later. The results of normals in the arrow probe task used here could also be attributed to automatic attraction of attention to the location of the feature target. When it appeared shortly after the feature search display it facilitated arrow detection perhaps due to the congruency of the arrow's orientation and the direction attention had previously moved when the search display appeared. However, in this model attention would need to encode the location of the feature target in order for attention to know where to go. R.M. could not explicitly locate the feature target in the briefly presented search display nor could he report the spatial relationship between the orientation of the arrow and the target when the display was presented for as long as he needed. The fact that his arrow probe responses were influenced by the location of the feature target is consistent with the existence of a separate spatial map outside the parietal lobes that directs attention automatically. The present data demonstrate that this spatial map does not require conscious awareness and continues to exert influence implicitly even in the face of severe explicit spatial deficits.

For R.M. computations of space are severely compromised producing deficits in spatial representations used for serial attentional search, for individuation of objects, and for proper feature binding in multiple item arrays (Robertson et al, 1997; Friedman-Hill et al, 1995). These effects of parietal lesions are all consistent with neurobiological evidence for dorsal processing of spatial information (Ungerleider & Mishkin, 1982). The present results demonstrate that the dorsal system (at least the occipital–parietal portion) is necessary for conscious awareness of space but is not necessary for the implicit encoding of space.

The present findings are also consistent with predictions of feature integration theory, which proposes a critical role for controlled spatial attention in feature binding, and thus conjunction search (Treisman & Gelade, 1980) but not in feature search. The implicit spatial maps that function for R.M. appear sufficiently complex to code a feature's *location*, its relationship to the *orientation* of an arrow, and its *spatial relationship* to other items in the display (i.e., the spatial configuration of the search display as a whole) but they are not sufficient to bind features properly in multi-item displays. Explicit access seems to be required.

Graziano and Gross (1996) suggested that parietal lobes function as a type of hub, selecting the proper spatial representation for the task at hand. They have reported several findings in awake, behaving monkeys demonstrating the existence of spatial neural responses in areas outside the parietal lobe. Whether or not these maps can influence performance implicitly is not known, but the present results suggest they may. The present results demonstrate that spatial information below the

level of awareness can exert control in humans without input from parietal areas that are critically involved in explicit spatial function (Colby, 1991; Andersen, 1987). The present results may reflect a computationally distinct spatial map dissociated from occipital–parietal areas or it may reflect an inability to access spatial maps outside these areas, bringing them to the level of spatial awareness. In either case the loss of explicit spatial awareness has devastating effects on perception, attention and awareness.

In sum, the present results demonstrate that implicit spatial coding can remain intact even when explicit spatial deficits are severe. Intact occipital–parietal function are necessary to explicitly represent spatial information that is used for purposes of volitionally guiding spatial attention and action. Spatial representations that remain below the level of awareness after parietal damage are sufficient to represent spatial configurations in multiple item displays. However, these spatial representations do not appear to be adequate for normal binding of features that are distributed in the visual cortex such as color and shape. The present findings are consistent with proposals for a complex system of spatial representations in the primate brain containing multiple spatial maps that support different functions (Graziano & Gross, 1996; Stein, 1992). They suggest that some may function without spatial awareness, while parietal lobes are necessary to explicitly perceive the spatial structure of the visual world.

METHODS

Experiment 1

Thirteen normal college students from the University of California, Berkeley, were tested in a single session and received course credit for their participation. R.M. was tested in the same paradigm in eight sessions to provide adequate statistical power to perform a single subject analysis. He was paid US\$10.00/hr for participation. All participants had normal or corrected to normal visual acuity (including R.M.) and gave informed consent before testing began.

A dual task was employed in which a search display was presented followed by a probe. Each item of the search display appeared around fixation, while the probe (an arrow) appeared centrally. Participants were instructed to respond as rapidly as possible to the appearance of the arrow shape and then report whether a feature target had appeared or not in the prior search display (Figure 1). The dependent measures were the errors and RT to detect the arrow probe and errors in detecting the presence or absence of the feature target. RTs were analyzed as a function of whether the arrow pointed to where a feature target or distractor had appeared in the prior search display. It either pointed to the target location (0°), to a distractor location 90°

from the target location, or to the distractor location 180° or opposite the target location.

Half the trials consisted of a four-item feature search display containing one green (or red) circle target and three red (or green) circle distractors with a central fixation pattern that changed into an arrow either 60 or 300 msec after search display offset. On the remaining trials the circles were all the same color. Stimuli were presented against a white background. One search item appeared in each quadrant, equally spaced in a square configuration around a fixation pattern. With a viewing distance of 58 cm, the whole array spanned approximately 9.8° visual angle. Each search shape approximated 1.8° visual angle. The center-to-center distance between elements was approximately 5.6°.

At the beginning of each trial, a fixation pattern appeared at the center of the screen for 1 sec. The search display then flashed for 60 msec. Following either 120 or 360 msec after search display onset (stimulus onset asynchrony or SOA), the fixation shape changed into an arrow probe that could point in one of four directions or it changed into a symmetrical star shape and response was to be withheld. Two-thirds of the trials contained arrows. The four directions of the arrow probe were equiprobable. The probe remained visible for 300 msec for R.M. and 60 msec for normal participants. The extra time for R.M. was necessary for him to discriminate the probe pattern above 90%. After responding to the arrow or after a fixed interval had passed with no response a display appeared alerting participants to verbally report whether a search target had been present or not in the search display on that trial. R.M. performed eight sessions of 72 trials each (576 trials overall) and with a 93% accuracy rate in responses to the arrow probe (used to calculate RTs), while normal participants performed 192 trials in one session with 98% accuracy overall.

Experiment 2

Feature or conjunction search displays were presented in separate blocks of trials. Only R.M. participated in this experiment and the probe was eliminated. Each display consisted of eight colored items arranged in a circle equally spaced around a central fixation point. Each search shape approximated 1.8° visual angle with the whole display spanning 10.8°. Center-to-center distance between elements was approximately 3.4°. The task was to report verbally the presence or absence of a red circle among green circle distractors in feature search and a red X among red Os and green Xs in conjunction search. The displays were shown for 160 msec following a 1-sec fixation, and R.M. was told to respond “yes” only when he was confident he saw the target. Each search task included 128 trials and was blocked. On half the trials a target was present, and on half it was absent.

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