Combined Expectancies: Event-Related Potentials Reveal the Early Benefits of Spatial Attention That Are Obscured by Reaction Time Measures

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Visual spatial attention has been likened to a "spotlight" that selectively facilitates the perceptual processing of events at covertly attended locations. However, if participants have advance knowledge of the likely location of an impending target and the likely response it will require, facilitation in response performance does not occur for targets at the expected (or attended) location that require an unexpected response. Event-related potentials (ERPs) were recorded during a discrimination task in which the most likely target location and target response were simultaneously cued prior to target onset. The ERPs showed evidence of enhanced perceptual-level processing for all targets at attended locations. These results suggest that the lack of response facilitation for unexpected targets at attended locations is likely due to postperceptual processes that are activated by the inclusion of nonspatial stimulus expectancies, response expectancies, or both.

Orienting visual spatial attention to the location of an impending target stimulus facilitates reaction times (RTs) to the target, compared with when targets are presented in unattended visual locations (e.g., Eriksen & Hoffman, 1972; Jonides, 1981; Posner, 1980; for a review, see Klein, Kingstone, & Pontefract, 1992). It has been suggested that the improved response performance associated with spatial attention may be restricted to effects on post-perceptual processing stages (e.g., Sperling, 1984; Sperling & Dosher, 1986), where attention may act to reduce potential noise in decision making (see Pashler, 1998; Shiu & Pashler, 1994). Al-

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This research was supported by Grants MH57138 and MH55714 from the National Institute of Mental Health, Grant 2-PO1-1778 from the National Institute of Neurological Disorders and Strokes, and a University of California, Davis Graduate Research Award. We thank Alan Kingstone, Martin Eimer, and Gregory DiGirolamo for many helpful comments on an earlier version of this article; Jason Ivanoff for discussions regarding the Simon effect; and Michael Gazzaniga, Jon Hansen, and Clif Kussmaul for their technical support.

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though attention may indeed have such postperceptual effects, evidence from studies using signal detection methodology have nevertheless shown that stimuli falling within an attended spatial region receive facilitated perceptual-level processing relative to stimuli presented outside of the attended region (e.g., Downing, 1988; Handy, Kingstone, & Mangun, 1996; Hawkins et al., 1990; Müller & Humphreys, 1991). Such evidence has lent strong support to the position that—at perceptual-level processing stages—spatial attention is analogous to a "spotlight" (Posner, 1980) or "zoom-lens" (Eriksen & St. James, 1986) that selectively enhances the processing of all stimuli falling within its zone of focus.

However, an important exception to this pattern of perceptual facilitation has been noted in the behavioral literature. In particular, studies of multiple or combined stimulus expectancies have suggested that all stimuli falling within the spotlight focus may not always receive the processing benefits associated with focused spatial attention. In combined expectancy experiments, participants are typically given advance knowledge of two highprobability aspects of an impending target, such as the most likely location of the target and the most likely response that it will require. Under these conditions, whether or not facilitation in behavioral performance arises for targets at the likely (i.e., attended) location appears to depend on the status of the nonspatial attribute: Whereas targets that have the expected nonspatial attribute receive the processing benefits characteristically afforded by spatial attention, such facilitation is absent for targets that have the unexpected nonspatial attribute. In the following article, we examine the electrophysiological correlates of this combined expectancy data pattern to determine if a reevaluation of the spotlight model is warranted.

The Combined Expectancy Data

The apparent contradiction to the spotlight model exposed by combined stimulus expectancies was first reported by Klein (1980) in a pair of dual-task experiments examining the relationship between spatial attention and eye movements. In the critical second experiment of this study, participants were cued to the most likely location-to the left or right of fixation-of an impending target on a trial-by-trial basis, where a small dot served as the target location marker in each visual hemifield. Within each block of trials, however, there were two different target types, which had different probabilities of occurrence and which required different overt responses. The more frequent target was the brief brightening of one of the location markers, a target that required a manual response in the form of a button release. The less frequent target was the presentation of an asterisk superimposed over one of the location markers, a target that required a saccadic response. Klein (1980) found that although manual responses to the targets at the expected location were quicker than those to targets at the unexpected location, the speed of saccadic responses were entirely unaffected by whether or not the asterisk target was presented at the expected location. These results suggested that although the likely targets (brightening dots) received the benefits of spatial attention at the attended location, the unlikely targets (asterisks) did not.

Klein's (1980) initial findings, which paired a trial-by-trial stimulus expectancy (location) with a blocked response expectancy (frequent manual response vs. infrequent saccadic response), have now been extended in two important ways. First, the data pattern holds independent of whether the unlikely response is saccadic or manual (Klein & Hansen, 1987, 1990). Second, a similar data pattern emerges if the location expectancy is combined with a target form expectancy, wherein participants are cued to the most likely shape or orientation of the impending target—an expectancy that is dissociated from the overt response that the target requires (e.g., Kingstone, 1992; Lambert, 1987; Lambert & Hockey, 1986). However, whereas unlikely responses effectively eliminated any RT facilitation for targets at the expected location, the manipulation of form expectancy only reduced RT facilitation for targets of the unexpected form at the expected location. In other words, when a form expectancy was coupled with a location expectancy, the interaction between the expectancies was weaker relative to when a location expectancy was coupled with a response expectancy. As an initial effort to disentangle these different effects, the current study focuses on how response expectancies interact with location expectancies; we return to a consideration of form expectancies in the General Discussion section.

Reported in Table 1 are the RT and error rate data from several combined location and response expectancy experiments. The pattern of results in Table 1 closely mirrors the original finding of Klein (1980), with unexpected target types—requiring the unexpected response—at the cued location not reliably showing the processing benefits typically afforded by the attentional spotlight. As can be seen, the location cuing effects in RT were consistently reduced or absent when target responses were unexpected. The

Table 1
Mean Reaction Times (RTs; in Milliseconds) and Error Rates (ERs) for Target Responses in Three Previous Combined Expectancy Experiments, as a Function of Expected Location and Response

	-	d location:	Unexpected location: Response		
Experiment & measure	Expected	Unexpected	Expected	Unexpected	
Klein & Hansen (1990)					
Experiment 1					
ŘТ	530	614	605	641	
ER	.015	.091	.037	.053	
Klein & Hansen (1990)					
Experiment 2					
ŘТ	545	646	599	660	
ER	.014	.071	.011	.029	
Klein (1994)					
Experiment 1					
ŘТ	448	524	506	533	
ER	.007	.060	.036	.034	
Arithmetic means of					
the above					
experiments					
RT	508	595	570	611	
ER	.012	.074	.028	.039	

Note. These data reveal that (a) when comparing between expected and unexpected locations, the response facilitation associated with the expected location is significantly reduced when the target requires an unexpected response (relative to targets requiring an expected response) and (b) error rates are consistently higher for targets requiring unexpected responses at the expected location, relative to all other expectancy conditions.

data in Table 1 also show that error rates are highest for targets requiring the unexpected response at the attended location. This suggests that in addition to the slowing of responses, participants have a tendency to give the expected response for the attended-but-unexpected targets. We next consider the two competing hypotheses that have been proposed to explain these RT and accuracy data.

Spotlight Failure

Initially, Klein (1980) hypothesized that the lack of response facilitation for the unexpected targets at the attended location may have been caused by failure of the spatial attention spotlight, where "the subject's attention may be allocated not to a position in visual space but to the set of known properties of the expected (primed) stimulus" (p. 274). In short, Klein argued that attention may mimic a spotlight when location is the only expected stimulus attribute,

¹ Specifically, when form expectancies were manipulated by Kingstone (1992, Experiments 1 & 2) and Lambert and Hockey (1986, Experiment 1), RT facilitation for targets of the unexpected form at the expected location was approximately one half of the RT facilitation seen for targets of the expected form at the expected location. In comparison, when response expectancies were manipulated in the studies by Klein (1994) and Klein and Hansen (1987, 1990), RT facilitation for targets requiring the unexpected response at the expected location was approximately one sixth of the facilitation seen for targets at the expected location that also required the expected response.

but when multiple expectancies are involved, attention may be directed to the conjunction of likely attributes, thereby eliminating any apparent benefits uniquely attributable to spatial attention. From this perspective, the spotlight metaphor may not hold during combined expectancies—a hypothesis that we refer to as *spotlight failure*.

A similar view was outlined by Kingstone (1992), following a series of experiments that compared the effects of combined location and form expectancies with conditions where advance knowledge of form was paired with advance knowledge of either color (Experiment 5) or time (Experiment 4). Kingstone found that the RT pattern characteristic of form-location expectancy interactions also arose in the form-color and form-time expectancy conditions: There was a significant increase in RT when a target having the unexpected form was presented in an expected location, color, or time, relative to when the target had the expected form. These results suggested that the effect of a location expectancy on RT was no different from the effects associated with color and time expectancies. Although Kingstone (1992) raised the possibility that the spatial attention spotlight may not operate when a location expectancy is paired with a second expectancy (i.e., spotlight failure may occur), he ultimately favored an alternative proposal: The combined expectancy interactions may reflect a postspotlight cross talk between systems that code different stimulus dimensions. In this scenario, form processing may be influenced by location, color, and time information because, as Kingstone showed, those stimulus attributes appear to be resolved more rapidly than form information.

Postspotlight Masking

Although the data patterns in Table 1 are consistent with the spotlight failure hypothesis, the studies discussed above converged on a second possibility as well: The spotlight may enhance early processing for all stimuli at the attended location, but the benefit afforded to unlikely stimuli at the attended location may be overshadowed or masked by events at a subsequent processing stage. This possibility is akin to the pigeonholing operations discussed by Broadbent (1971). Specifically, in the context of combined expectancies, participants' responses to unlikely stimuli at the expected location may be slowed because of the initial tendency to categorize (or pigeonhole) them—based on the response expectancy—as the likely stimulus. In this scenario the spotlight facilitates the processing of all targets at the expected location, but there is a cost in RT for the unlikely targets at response-level processing stages due to reprogramming the unanticipated response. The increased error rate characteristic of unexpected targets at expected locations lends support to this position in that it may reflect a difficulty participants have in withholding the expected response whenever targets are presented in the attended location. Modifying the term used by Klein and Hansen (1990), we refer to this hypothesis as postspotlight masking.²

A formal logogen activation model of how postspotlight masking may arise via a pigeonholing-type operation was developed by Klein and Hansen (1990) to simulate the performance data from their combined expectancy experiments. In brief, on the input side were four stimulus logogens representing each of the possible target conditions: Expected location/expected target, expected location/unexpected target, unexpected location/expected target, and

unexpected location/unexpected target. On the output side were two response logogens, one for each of the two possible response options, which received postthreshold input from the stimulus logogens; a response was assumed to be made when one of these two response logogens exceeded threshold. Importantly, the thresholds for the input and output logogens were negatively related to the probability of stimulus and response occurrence (i.e., the higher the probability of a stimulus or response, the lower the threshold in the corresponding logogen).

During simulated performance, each cycle consisted of giving noise to each stimulus logogen and an input signal (S) to the logogen corresponding to the target type and location. However, it was assumed that at the target location, the target identity was confusable. Accordingly, although the logogen for the appropriate (or presented) stimulus and location received input signal S, the logogen for the inappropriate (or not presented) stimulus at the appropriate location was given an input signal that was less thanbut a constant proportion of—S. The spotlight effect for targets at the expected (or attended) location was then implemented as an increase in S whenever the target was presented at the expected location. Using this framework to model their performance data, Klein and Hansen (1990) demonstrated that the lack of RT facilitation and the increased error rate for unlikely targets at the attended location could be produced in two different ways: by a signal enhancement for the expected location (i.e., the spotlight effect) that occurs in conjunction with a lowered (or biased) response threshold for the likely response or by the biased response threshold alone. As a result, it remained unclear as to whether the spotlight effect for unexpected targets at the expected location was masked by subsequent response-related processes or whether no spotlight facilitation had occurred under that stimulus condition.

Resolving the Debate—An Event-Related Potential Approach

Unlike spotlight failure, the postspotlight masking hypothesis has the advantage of remaining consistent with the canonical model that spatial attention will facilitate the perceptual processing of all stimuli falling within an attended location. However, as noted above, the performance data remain equivocal on this issue, and it may be difficult to resolve the debate between these competing hypotheses relying on RT and accuracy measures alone. The issue remains critical because should spotlight failure prove to be the correct account of the combined expectancy phenomenon, it would pose a serious challenge to current conventions regarding spatial attention and the mechanisms underlying early spatial selection. Specifically, much evidence has accrued in recent years indicating that when attention is allocated to a discrete location in the visual field, the initial processing of information at that location is selectively enhanced (e.g., an increase in sensory gain) relative to information arising outside of the attentional focus (for

² The original term used by Klein and Hansen (1990) was "spotlight masking." We are adopting the term *postspotlight masking* to emphasize that this hypothesis posits that the initial spotlight facilitates all events at the attended/expected target location and that the lack of RT facilitation for unexpected targets at this location is caused by processing that occurs after the locus of this spotlight effect.

a review, see Mangun, 1995). In contrast, the spotlight failure hypothesis would suggest that when multiple expectancies are invoked, such early, spatial-based selection should only occur for stimuli congruent with all current expectancies. The difficulty of this position stems from trying to reconcile the operation of initial spatial selection mechanisms affecting early sensory processing with later stimulus- and response-related expectancies.

One approach for addressing the current question is to directly measure the cortical processing of stimuli under conditions of combined location and response expectancies. In particular, eventrelated potentials (ERPs) can be used to index the temporal dynamics of stimulus processing in cortex with a millisecondlevel resolution (see Coles & Rugg, 1995). Using these electrophysiological-based measures, a number of studies have shown that when visual stimuli are presented in an attended spatial location, the amplitudes of the lateral occipital P1 and N1 (e.g., Eason, 1981; Handy & Mangun, 2000; Luck et al., 1994; Mangun & Hillyard, 1991; Van Voorhis & Hillyard, 1977) and occipitoparietal N1 (e.g., Eimer, 1994, 1998) components are larger, relative to when the same stimuli are presented in unattended spatial locations. These findings have been taken as evidence that the benefits in response performance that are associated with spatial attention are accompanied by enhanced sensory/perceptual-level processing in extrastriate visual cortex (for reviews, see Mangun, 1995; Hillyard & Mangun, 1995). As a result, ERPs can be recorded during combined expectancies to examine whether unexpected targets at attended locations show this ERP signature of attention-related enhancement in extrastriate processing. If so, it would support the postspotlight masking hypothesis of combined expectancies. If not, it would support the spotlight failure hypothesis.

Adopting this ERP approach, we performed two experiments to resolve whether combined expectancies lead to spotlight failure or masking. In Experiment 1, we established the baseline behavioral pattern of combined location and response expectancies. In Experiment 2, we used the identical paradigm while recording ERP measures, thereby allowing a direct comparison between the behavioral pattern characteristic of combined expectancies and the underlying electrophysiological correlates.

Experiment 1

As outlined above, the pigeonholing model of postspotlight masking suggests that-during combined location and response expectancies-the longer RT and decreased accuracy for unexpected targets at the attended location are due to postperceptual processing that obscures the initial perceptual facilitation afforded by spatial attention. In contrast, the spotlight failure hypothesis holds that these benefits of spatial attention are not afforded to unexpected stimuli at expected locations. In Experiment 1, we established the behavioral pattern of combined expectancies by using trial-by-trial cuing of both location and response expectancies. On every trial, participants were cued to the most likely location (left or right of fixation) and orientation (vertical or horizontal) of an impending square-wave grating stimulus, with the task being a choice discrimination of the grating orientation. In this manner, the cuing of target orientation served to generate a response expectancy.³ The speed and accuracy of responses were recorded as a function of target location (expected vs. unexpected) and orientation (expected vs. unexpected).

Method

Participants

Ten members (7 women, 3 men) of the University of California, Davis, community between the ages of 20 and 32 were recruited as paid participants. All were right-handed and had normal or corrected-to-normal vision.

Apparatus and Stimuli

Stimuli were presented on a 15" NEC 4FG color monitor placed 100 cm from the participant and were controlled by a 486-based microcomputer using VGA graphics. Each trial began with the presentation of an arrow (.7° long) at fixation that cued the most likely location of the impending target grating. Positioned directly above the arrow and presented simultaneously, a letter cue (V or H, .23° tall \times .23° wide) was used to indicate the most likely orientation (vertical or horizontal) of the grating. Together the cues were presented for 200 ms. Following a randomly varied interstimulus interval of 600-800 ms (uniformly distributed), a target grating was presented in the lower visual field, to the left or right of fixation, for 100 ms. These gratings were square waves of 2 cycles per degree, with alternating black and white bars that formed a 2° square. Small white dots were used in the display background to mark the center of the target location in each visual hemifield. These location markers were 4.6° to the left or right of fixation and 1.4° below the horizontal meridian. As a result, the gratings were presented in each hemifield 4.8° from fixation, to center. The fixation point was white, and the background was a medium shade of gray (VGA rgb intensities: 35, 35, 35). The intertrial interval—from target offset to cue onset-was 2,000 ms; as such, each block of trials proceeded in an automatic fashion, independent of the participants' responses to the targets. A schematic representation of the trial sequence is shown in Figure 1.

Procedure

The task required participants to make a forced, two-choice decision regarding the orientation of the target grating on each trial (vertical or horizontal). Participants responded by pressing the appropriate response button located on a hand-held computer joystick; they indicated vertical with one thumb and horizontal with the other thumb. The mapping of response option (vertical vs. horizontal) and thumb of response (right vs. left) was counterbalanced between subjects such that half of the participants responded vertical with the left thumb and horizontal with the right thumb, and half the participants had the opposite response mapping. Instructions were given to maintain gaze on the fixation point for the duration of each trial block. Participants were also told that the arrow cue would indicate the most likely location of the subsequent target and that the letter cue would indicate the most likely orientation of the grating. They were encouraged to use this information to maximize both the speed and accuracy of their responses to the targets.

Trials with anticipatory (<150 ms) or delayed (>1,500 ms) responses were not included in the data reported below. Because trials proceeded at

³ It is important to note that using form cuing to manipulate response expectancy differs from the form cuing used by Kingstone (1992), who dissociated form expectancies from response expectancies. In the General Discussion, we take up the issue of how form expectancies compare to response expectancies, when each are selectively combined with location cuing.

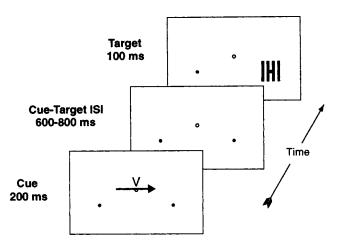


Figure 1. Sequence and timing of stimulus events presented on each trial in Experiments 1 and 2. In the trial shown, both location and orientation of the target are cued. ISI stands for interstimulus interval, and the intertrial interval was 2,000 ms. Stimuli are not to scale and are shown in reverse contrast to that actually used in the experiments.

a fixed temporal rate, trials that had an overlapped response from the previous trial (i.e., when a response from the previous trial was >2,000 ms) were also excluded from analysis. Across participants, less than 2% of the total number of trials were eliminated on the basis of these response-latency criteria. In addition to practice, participants were run in 15 blocks of 60 trials, with each block lasting about 3 min. Within each block of 60 trials, on 48 trials both location and orientation were validly cued; on 4 trials only location was validly cued; on 4 trials only orientation was validly cued; and on 4 trials neither location or orientation were validly cued. As a result, each cue was .867 predictive of its specific stimulus attribute (i.e., 52 trials out of 60). Each block of trials contained all possible combinations of target locations and orientations in each cue-validity combination.

To ensure proper eye fixation, we recorded vertical and horizontal electro-oculograms (EOGs), amplified with a gain of 50,000, band-pass filtered from .1 to 100 Hz, and digitized at 256 samples per second. The vertical EOG was recorded from an electrode inferior to the right eye, and the horizontal EOG was recorded from an electrode on the right outer canthus; both of these electrodes were referenced to an electrode on the left mastoid. We used on-line monitoring of the EOGs to control for large eye movements by providing feedback to the participant by the investigator, as needed. Off-line, trials were rejected that contained eye movement or blink artifacts, and subsequent signal averaging to the onset of the location cue allowed for the detection of very small (<0.36°) systematic eye movements (see Mangun & Hillyard, 1991, Experiment 4). For each participant, we established the threshold for rejection by comparing the magnitude of their blink and movement artifacts on the EOG with the baseline level of their EOG when no artifacts were occurring; threshold was then set on each EOG channel to fall in between these approximated baseline and artifact levels. On average, about 5% of each participant's total number of trials were rejected for these eye-related artifacts.

We computed the error rate data reported below for each combination of cuing condition by dividing the number of incorrect responses (i.e., a vertical response for a horizontal target or a horizontal response for a vertical target) by the total number of trials in which a response was made. We do not report data on trials in which no responses were made (i.e., misses); because of the analysis procedure, trials that engendered no response could not be distinguished from trials that were rejected for blink and eye movement artifacts. However, on-line monitoring of behavioral

performance indicated that overall misses were very low (<1% of total trials).

Results

RTs

Mean RTs across participants for each of the four possible cuing conditions are reported in the upper half of Table 2. The RTs replicate the basic finding for combined expectancies by showing that location cuing only affected the speed of response when the target had the expected orientation. This finding was supported by an omnibus repeated measures analysis of variance (ANOVA) that had factors of target location (expected vs. unexpected) and target orientation (expected vs. unexpected): There were main effects of both location expectancy, F(1, 9) = 52.64, p < .001, and orientation expectancy, F(1, 9) = 110.71, p < .001, and a Location \times Orientation interaction, F(1, 9) = 47.64, p < .001. Planned comparisons using two-tailed t tests confirmed that when orientation was validly cued, RTs were significantly shorter when the expected target was at the expected location, in comparison to when it was at the unexpected location, t(9) = -7.61, p < .001. Conversely, when the target orientation was invalidly cued, RTs were unaffected by whether the unexpected target was at the expected or unexpected location, t(9) = -1.11, p > .25.

Error Rate

Mean error rates are reported in the lower half of Table 2. Consistent with the RT data, the omnibus repeated measures ANOVA showed significant main effects of both location expectancy, F(1, 9) = 8.95, p < .05, and orientation expectancy, F(1, 9) = 18.28, p < .005, and a Location × Orientation interaction, F(1, 9) = 16.12, p < .005. Planned comparisons showed that when the target had the expected orientation, there were marginally fewer errors when the expected target was at the expected location, relative to when it was at the unexpected location, t(9) = -1.96, p < .10. In contrast, when the target had the unexpected orientation, there were significantly more errors when the unexpected target was at the expected location, relative to when it was at the unexpected location, t(9) = -3.53, p < .01.

Discussion

The pattern of response performance found in Experiment 1 closely replicates what has been obtained in prior studies of

Table 2
Mean Reaction Times (RTs, in Milliseconds) and Error Rates
(ERs) for Target Responses in Experiment 1, as a Function of
Orientation and Location Expectancies

	L		expected tation	l: 	Lo	Location unexpected: Orientation			
	Expe	cted	Unexp	ected	Expe	cted	Unexp	ected	
Measure	М	SD	М	SD	M	SD	М	SD	
RT ER	361 .016	67 .01	496 .227	63 .16	440 .033	68 .02	500 .054	60 .05	

combined location and response expectancies (e.g., Klein, 1994; Klein & Hansen, 1987, 1990). On trials when the target had the expected orientation, the normal effect of location expectancy was found, with RTs for the expected targets being shorter when they were at the expected location as compared with the unexpected location. In contrast, when targets had the unexpected orientation, RTs to the unexpected targets were unaffected by the location expectancy, with comparable RTs when they were at either the expected or unexpected location. In terms of how response expectancy affected the speed of processing for targets at the attended location, this RT pattern was consistent with the pattern of results from prior combined expectancy studies, as shown in Table 1. Likewise, typical combined-expectancy effects were also observed in the accuracy data. When targets with an unexpected orientation were presented at the expected location, participants had difficulty withholding the expected response, as indicated by the significantly greater error rate for those targets-an effect on error rate that replicates the pattern found in previous studies that also collapsed form and response expectancies (e.g., Klein & Hansen, 1987, 1990; see Table 1). Importantly, although prior studies of combined location and response expectancies have used blocked response expectancies (Klein, 1980, 1994; Klein & Hansen, 1987, 1990), the results of Experiment 1 demonstrate that a similar pattern emerges if response expectancies are manipulated on a trial-by-trial basis.

One concern about the current paradigm is that using a letter to cue response expectancy while using a nonletter (i.e., an arrow) to cue location expectancy opens the possibility that the cues may have been encoded at different rates, thereby systematically skewing the intensities of the expectancies that were generated on each trial. Although it may be difficult to quantify the magnitude of the participants' expectancies, two lines of evidence suggest that they were sufficient for affecting stimulus processing. First, significant main effects of location and response expectancies were found in the behavioral data. Second, the behavioral data closely replicate the data patterns observed in prior studies of combined expectancies, studies that have used various expectancy manipulations in both blocked and trial-by-trial designs (e.g., Kingstone, 1992; Klein, 1980, 1994; Klein & Hansen, 1990; Lambert, 1987; Lambert & Hockey, 1986). Taken together, this suggests that the results of the current study were not confounded by the differences in dimensional aspects of the two expectancy cues. Rather, that the combined expectancy pattern in RT and error rates remains consistent across a wide variety of paradigms is a strong testament to the robustness of the effect.

Regardless, to determine whether this behavioral pattern for unexpected responses at the expected location is caused by spotlight failure or postspotlight masking, we performed a second experiment that used ERP measures to directly index the cortical processing of target stimuli during combined location and response expectancies.

Experiment 2

Studies using ERPs have shown that the amplitudes of the sensory-evoked, lateral occipital P1 and N1 ERP components are larger for stimuli in attended versus unattended locations, which has been taken as prima facie evidence that stimuli falling within the spotlight of spatial attention are subject to increases in sensory

gain (for reviews, see Mangun, 1995; Mangun & Hillyard, 1995). If combined location and response expectancies lead to spotlight failure for unexpected targets at the expected location, the amplitudes of the P1 and N1 should be largest when expected targets are presented in the expected location. In comparison, the P1 and N1 amplitudes should be equivalent and smaller for unexpected targets at the expected location and all targets at the unexpected location. However, if combined expectancies lead to postspotlight masking, then the amplitudes of the P1 and N1 should be equivalent for all targets at the expected location—and larger in comparison to all targets at the unexpected location.

Method

Participants

Eight members (4 women, 4 men) of the University of California, Davis, community between the ages of 20 and 33 were recruited as paid participants. All were right-handed and had normal or corrected-to-normal vision. Four of the participants who volunteered for this experiment had also participated in Experiment 1.

Stimuli and Procedure

All stimuli and procedures were identical to Experiment 1, with the following exceptions: Participants were run in a total of 25 trial blocks of 60 trials each, and ERPs were recorded.

Electrophysiological Recording

We recorded scalp potentials using tin electrodes mounted in a custom elastic cap. Electrodes were located at sites FP1, FP2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T3, T4, T5, T6, CZ, FZ, and PZ of the International 10-20 System and from 10 nonstandard sites: OZ (midway between O1 and O2), POZ (midway between OZ and PZ), OL and OR (midway between T5 & O1 and T6 & O2, respectively), P1 and P2 (midway between P3 & PZ and P4 & PZ, respectively), P5 and P6 (midway between T5 & P3 and T6 & P4, respectively), and PO1 and PO2 (midway between O1 & P1 and O2 & P2, respectively), along with an electrode on the right mastoid process (used for off-line re-referencing; see below). During recording, these electrodes were referenced to an electrode on the left mastoid process. All electroencephalographic (EEG) activity was amplified with a band-pass of 0.1-100 Hz (1/2 amplitude cutoffs), digitized on-line at a sampling rate of 256 samples per second, and stored on hard disk. Off-line, we used computerized artifact rejection to eliminate trials during which large eye movements (>1°), blinks, muscle potentials, or amplifier blocking occurred. EOG recording and analyses were identical to those reported in Experiment 1.

During analysis, for each participant ERPs to the targets were averaged into 3,000-ms epochs, beginning 1,500 ms before target onset and ending 1,400 ms after target offset (the target was present for 100 ms). Subsequently, all ERPs were algebraically re-referenced to the average of the left and right mastoid signals and were filtered with a low-pass Gaussian filter (a Gaussian impulse-response function with a standard deviation of 8 ms and a half-amplitude cutoff of 10 Hz) to eliminate high-frequency artifacts in the waveforms. We then used the resulting ERPs to produce the grand-averaged waveforms presented below.

Results

RTs

Mean RTs across participants for each of the four possible cuing conditions are reported in the upper half of Table 3. Again, when

Table 3
Mean Reaction Times (RTs; in Milliseconds) and Error Rates (ERs) for Target Responses in Experiment 2, as a Function of Orientation and Location Expectancy

	L		expected tation	l: 	Loc	cation u Orien	nexpected: tation	
	Expe	cted	Unexp	ected	Expe	cted	Unexp	ected
Measure	М	SD	M	SD	М	SD	М	SD
RT ER	394 .017	74 .01	510 .193	52 .15	466 .021	66 .02	510 .046	58 .04

target orientation was validly cued, RTs were longer when the expected target was at the unexpected location, relative to when it was at the expected location. This result was shown in the omnibus repeated measures ANOVA by main effects of both location expectancy, F(1, 7) = 235.50, p < .001, and orientation expectancy, F(1, 7) = 31.34, p < .001, and a Location × Orientation interaction, F(1, 7) = 15.34, p < .01. Planned comparisons using two-tailed t tests confirmed that when orientation was validly cued, RTs were significantly shorter for the expected targets at the expected location than at the unexpected location, t(7) = -6.65, p < .001. Conversely, when orientation was invalidly cued, RTs were equally long for the unexpected targets at the expected and unexpected locations, t(7) = -0.03.

Error Rate

Mean error rates across participants for each of the four possible cuing conditions are reported in the lower half of Table 3. Error rate was only affected by the location expectancy when the target orientation was unexpected. The omnibus repeated measures ANOVA showed significant main effects of both location expectancy, F(1, 7) = 8.50, p < .05, and orientation expectancy, F(1, 7) = 12.31, p < .01, and a Location \times Orientation interaction, F(1, 7) = 11.40, p < .05. Planned comparisons confirmed that when orientation was validly cued, error rates were comparable for the unexpected targets at the expected and unexpected locations, t(7) = -0.63. In contrast, when orientation was invalidly cued, error rates were significantly greater for the unexpected targets at the expected location than at unexpected location, t(7) = 3.16, p < .05.

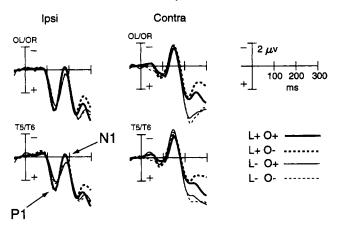
ERPs: Early Components

There are three components of interest in regards to the early effects of spatial attention, the lateral occipital P1 and N1 (e.g., Mangun & Hillyard, 1991) and the parietal N1 (e.g., Eimer, 1994). The contralateral and ipsilateral P1 and N1 ERP components from lateral occipital electrodes OL/OR and T5/T6 can be seen in the upper half of Figure 2 as a function of cue condition, and the mean amplitudes of these components are reported in Table 4. The central parietal N1 is shown in Figure 3 for midline electrode sites PZ and POZ, and the mean amplitudes of this component are reported in Table 5, also as a function of cue condition. As can be seen in Figure 2 (top) and Figure 3, the evidence for early enhancement in the lateral occipital P1 and N1 and the central

parietal N1 is equivalent at the expected location for targets having both the expected (the L+ O+ trace in Figures 2 & 3) and unexpected (L+ O-) orientations, with larger amplitudes in these conditions compared with the targets presented at the unexpected location (L- O+ and L- O-), as highlighted in the ERP difference waves shown in the bottom half of Figure 2.

Omnibus repeated measures ANOVAs performed on the lateral occipital P1 and N1 data included main factors of target location (expected vs. unexpected), target orientation (expected vs. unex-

Lateral Occipital ERPs



Difference Waves

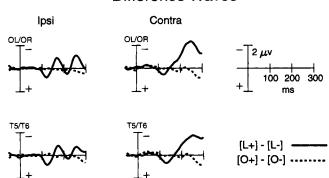


Figure 2. (Top) The lateral occipital P1 and N1 event-related potential (ERP) components from Experiment 2, averaged over the 8 participants, as a function of cued location and orientation (location cued: L+, location uncued: L-; orientation cued: O+; orientation uncued: O-). The ERPs are collapsed for visual field and are shown as a function of whether the target was in the visual field contralateral (contra) or ipsilateral (ipsi) to the hemisphere of recording. For targets in the left visual field, the ipsi electrodes are OL and T5, and the contra electrodes are OR and T6; for targets in the right visual field, the ipsi-contra mapping is reversed. The P1 and N1 components are labeled in the lower left plot. (Bottom). The difference waves of the P1 and N1 ERP components, as a function of hemisphere of recording. For location the L- traces from the ERPs above have been subtracted from the L+ traces, and for orientation the O- traces have been subtracted from the O+ traces. These difference waves show that processing varies as a function of spatial location (solid traces) well before any effects associated with orientation cuing arise (dashed traces).

Table 4
Mean Amplitudes in Microvolts (±SE) of the Lateral Occipital
P1 and N1 ERP Components in Experiment 2 to Targets, as a
Function of Orientation and Location Expectancy, and
Hemisphere of Recording (Contralateral vs. Ipsilateral)

	Location Orien		Location unexpected: Orientation		
ERP and electrode	Expected	Unexpected	Expected	Unexpected	
Ipsi P1					
OL/OR	$2.59 \pm .48$	$2.45 \pm .50$	$2.17 \pm .47$	$2.22 \pm .46$	
T5/T6	$1.93 \pm .36$	$1.90 \pm .40$	$1.35 \pm .38$	$1.50 \pm .32$	
Contra P1					
OL/OR	$0.34 \pm .34$	$0.60 \pm .31$	$0.37 \pm .39$	$0.36 \pm .38$	
T5/T6	$-0.02 \pm .27$	$0.27 \pm .26$	$0.04 \pm .31$	$0.01 \pm .33$	
Ipsi N1					
OL/OR	$0.51 \pm .38$	$0.25 \pm .46$	$0.88 \pm .38$	$0.89 \pm .36$	
T5/T6	$0.31 \pm .36$	$0.14 \pm .43$	$0.70 \pm .37$	$0.72 \pm .26$	
Contra N1					
OL/OR	$-1.08 \pm .45$	$-1.29 \pm .49$	$-1.37 \pm .58$	$-1.25 \pm .56$	
T5/T6	$-1.43 \pm .43$	$-1.62 \pm .30$	$-1.96 \pm .61$	$-1.92 \pm .54$	

Note. Time windows (in ms) were 60-110 (contra P1), 110-160 (ipsi P1), 125-175 (contra N1), and 155-205 (ipsi N1). ERP = event-related potential; Ipsi = ipsilateral; Contra = contralateral.

pected), visual field of target (left vs. right), hemisphere of electrode recording relative to visual field of target (ipsilateral vs. contralateral), and electrode site (T5/T6 vs. OL/OR). The omnibus ANOVA performed on the central parietal N1 differed only in that there was no factor of hemisphere, and the electrode sites were PZ and POZ. Taken together, these electrode sites were chosen a priori for analyses because the components of interest are consistently maximal at these locations. For each participant, the mean amplitudes of these early components were computed over a 50-ms time window (reported in Tables 4 and 5) centered approximately on the peak latency of each component in the grandaveraged waveforms. The baseline for these measurements was the mean voltage for the 100-ms interval preceding target onset. Because they ultimately had no bearing on the interpretation of the results given here, significant effects of electrode, visual field, and interactions involving these factors are not reported below.

Lateral occipital P1. Consistent with spotlight masking, the amplitude of the lateral occipital P1 was significantly larger for all targets at the expected location, relative to the targets at the unexpected location. This result was confirmed in the omnibus ANOVA by a significant main effect of location expectancy F(1,7) = 10.29, p < .05, without a main effect of orientation expectancy, F(1, 7) = 0.59, or Location \times Orientation interaction, F(1, 7) = 0.59, or Location 7) = 0.12. However, there was a marginal Hemisphere \times Location interaction, F(1, 7) = 3.60, p < .10, indicating that the location effect was more prominent in the ipsilateral hemisphere relative to the contralateral hemisphere, as can be seen in Figure 2 (top). There was also a main effect of hemisphere, F(1, 7) = 8.30, p <.05. To examine hemispheric differences more closely, we conducted additional ANOVAs within each hemisphere to confirm that there was a main effect of location expectancy in the ipsilateral hemisphere, F(1, 7) = 25.46, p < .005, but not the contralateral hemisphere, F(1, 7) = 0.53, p > .10.

Lateral occipital N1. The amplitude of the lateral occipital N1 was also larger for all targets at the expected location, relative to

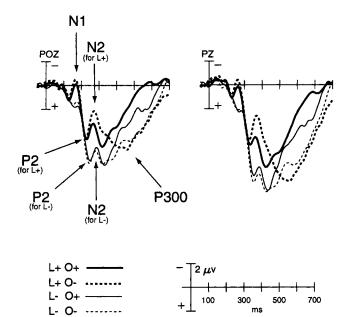


Figure 3. The central parietal N1, P2, N2, and P300 event-related potential (ERP) components from Experiment 2, averaged over the 8 participants, as a function of location and orientation cuing (location cued: L+, location uncued: L-; orientation cued: O+, orientation uncued: O-). The ERPs are collapsed for visual field. There are four things to note in these data: (1) the N1 is larger for targets at the cued location, (2) the latency of the P2 is earlier for targets at the cued location, (3) the N2 is more negative-going for targets at the cued location, an effect that increased at the cued location when target orientation was uncued (L+O- trace), and (4) the P300 is more prominent for targets of the uncued orientation.

targets at the unexpected location, but only in the ipsilateral hemisphere. This was confirmed in the omnibus ANOVA by a Hemisphere \times Location interaction, F(1, 7) = 5.49, p < .06, and nonsignificant effects of either location expectancy, F(1, 7) = 0.28, p > .10, or orientation expectancy, F(1, 7) = 0.63, p > .10. In addition, there was a main effect of hemisphere, F(1, 7) = 15.84, p < .01. However, additional ANOVAs looking at expectancy effects within each hemisphere failed to show a significant main effect of location expectancy within either the ipsilateral, F(1, 7) = 2.19, p > .10, or contralateral, F(1, 7) = 2.18, p > .10, hemisphere.

Table 5
Mean Amplitudes in Microvolts (±SE) of the Central Parietal
N1 ERP Component in Experiment 2 to Targets, as a
Function of Orientation and Location Expectancy

	Location expected: Orientation		Location unexpected: Orientation		
ERP and electrode	Expected	Unexpected	Expected	Unexpected	
N1					
PZ	$0.41 \pm .52$	$-0.07 \pm .58$	$1.61 \pm .74$	$1.91 \pm .73$	
POZ	$0.28 \pm .46$	$-0.09 \pm .47$	$1.37 \pm .58$	1.41 ± .65	

Note. The time window was 140-190 ms. ERP = event-related potential.

Central parietal N1. Like the other early components, the amplitude of the central parietal N1 was larger for all targets at the expected location—relative to the unexpected location—independent of whether or not the targets were of the expected orientation. This result was confirmed in the omnibus ANOVA by a main effect of location expectancy, F(1, 7) = 5.52, p < .06, with no effect of orientation expectancy, F(1, 7) = 0.37, p > .10, or Location × Orientation interaction, F(1, 7) = 2.25, p > .10.

ERPs: Late Components

The later components that were examined to detail the sequence of processing events subsequent to the initial effect of spatial attention were the midline parietal P2, N2, and P300. These ERP components from midline electrodes PZ and POZ can be seen in Figure 3 as a function of expectancy condition. There are at least four revealing effects within these data. First, the latency of the P2 peak was earlier for targets at the expected location (Table 6, top). Second, for targets at the expected location, the latency of the N2 peak was earlier for targets of the expected orientation, relative to targets of the unexpected orientation (Table 6, bottom). Third, for targets at the expected location, the mean amplitude of the N2 was greater (i.e., more negative/less positive) for targets of the unexpected orientation, as compared with targets of the expected orientation (Table 7). Finally, independent of the target location, the P300 was prominent for all targets of the unexpected orientation and was absent for all targets of the expected orientation (Table 8).4

The omnibus repeated measures ANOVAs performed on these late components included main factors of target location (expected vs. unexpected), target orientation (expected vs. unexpected), visual field of target (left vs. right), and electrode site (PZ vs. POZ). These electrode sites were chosen post hoc for analysis because on visual inspection of the data, the later effects of interest appeared to be largest in these midline parietal locations. The mean amplitude of the N2 was computed over a 50-ms time window, and the P300 was computed over a 100-ms window (reported in Tables 7 and 8, respectively), with both windows centered approximately on the peak latency of the component in the grand-averaged waveforms. The baseline for these amplitude measurements was the mean voltage for the 100-ms interval preceding stimulus onset.

Table 6
Peak Latency in Milliseconds (±SE) of the P2 (Top) and N2
(Bottom) ERP Component in Experiment 2 to Targets, as a
Function of Orientation and Location Expectancy

	Location expected: Orientation			inexpected:
ERP and electrode	Expected	Unexpected	Expected	Unexpected
P2				
PZ	238 ± 2.67	225 ± 5.16	247 ± 0.79	244 ± 2.01
POZ	232 ± 2.34	227 ± 3.52	241 ± 4.34	238 ± 4.46
N2				
PZ	262 ± 3.27	275 ± 3.41	275 ± 4.86	278 ± 4.79
POZ	268 ± 2.56	273 ± 3.47	279 ± 4.23	278 ± 4.49

Note. ERP = event-related potential.

Table 7
Mean Amplitude in Microvolts (±SE) of the N2 ERP
Component in Experiment 2 to Targets at the Expected
Location, as a Function of Orientation Expectancy

	Orien	ntation
ERP and electrode	Expected	Unexpected
N2		
PZ	$4.64 \pm .69$	$2.88 \pm .84$
POZ	3.51 ± .53	2.49 ± .70

Note. These data highlight that the N2 had a larger (more negative) amplitude for targets at the expected location when the orientation was unexpected. The time window was 245–295 ms. ERP = event-related potential.

P2 component. The notable aspect of this component was that the latency of the peak was significantly earlier for all targets at the expected location, in comparison to targets in the unexpected location. This result was confirmed in the omnibus ANOVA, which showed a main effect of location expectancy on the peak latency, F(1, 7) = 15.96, p < .01, with no effect of orientation expectancy, F(1, 7) = 3.83, p > .10, or Location \times Orientation interaction, F(1, 7) = 1.63, p > .10.

N2 component. The N2 manifest two important patterns. First, the latency of the peak was earlier for targets of the expected orientation at the expected location, relative to all other expectancy combinations. This result was confirmed in the omnibus ANOVA on the peak latency by a significant interaction between location and orientation expectancies, F(1, 7) = 7.69, p < .05, without an effect of location expectancy, F(1, 7) = 2.29, p > .10, but with a marginal effect of orientation expectancy, F(1, 7) = 3.89, p < .10. Second, for targets at the expected location, the amplitude of the N2 was more negative for targets that had the unexpected orientation, in comparison to targets that had the expected orientation, as can be seen in Figure 3 and Table 7. However, an additional ANOVA looking at only the expected location showed that this effect of orientation was only marginally significant at best when analyzed statistically, F(1, 7) = 4.09, p < .10.

P300 component. The P300 was prominent only when target orientation was unexpected. This result was confirmed in the omnibus ANOVA by a main effect of orientation expectancy, F(1, 7) = 16.70, p < .005. No main effect of location expectancy was found in the P300, F(1, 7) = 0.07, p < .10, nor was there a significant Location \times Orientation interaction, F(1, 7) = 2.14, p < .10.

Discussion

The behavioral results of Experiment 2 replicated the pattern found in Experiment 1 and are not discussed further here. Critically, the early ERP components reveal that initial processing in visual cortex—as indexed by the lateral occipital P1 and N1 and the midline parietal N1—was facilitated for targets at the expected location independent of whether the target orientation was also

⁴ We would like to thank Martin Eimer and Gregory DiGirolamo in particular for their help in interpreting these later ERP components.

Table 8

Mean Amplitude in Microvolts (±SE) of the P300 ERP

Component in Experiment 2 to Targets, as a Function
of Orientation and Location Expectancy

	Location expected: Orientation		Location unexpected: Orientation		
ERP and electrode	Expected	Unexpected	Expected	Unexpected	
P300 PZ POZ		7.65 ± .68 5.00 ± .43	4.68 ± .49 3.10 ± .50	6.81 ± .64 4.74 ± .56	

Note. The time window was 400-500 ms. ERP = event-related potential.

expected. That is, the amplitudes of these components were consistently larger for all targets at the expected location, showing the typical pattern of processing benefits associated with spatial attention (e.g., Eimer, 1994, 1998; Mangun, 1995; Mangun & Hillyard, 1995). Had the spotlight only favored targets at the expected location when orientation was also expected, an interaction would have been observed between these expectancy conditions.

One concern with the lateral occipital P1 and N1 data may be that the effects of spatial attention were lateralized to the ipsilateral hemisphere and were weaker in the N1 relative to the P1. However, recently it was shown that the magnitude of spatial attention effects in these two ERP components are dependent on the perceptual load of the target items used in the given task. In particular, attention-related amplitude modulations are found in both the ipsi and contra hemispheres when perceptual load is high, but these effects are limited to the ipsi hemisphere when load is low, and further, they may be less prominent in the ipsi N1 than in the ipsi P1 (Handy & Mangun, 2000)—a data pattern consistent with what was observed here. The ipsi/contra difference observed in Experiment 2 thus likely reflects the relatively low perceptual load of the targets used in this study, an assumption supported by the low error rates for all but the unexpected target at the expected location condition. Taken in this light, the early components in the ERP data provide evidence that supports the position that combined location and response expectancies lead to postspotlight masking, where early enhancement of signals from the expected location occurs independent of whether the target requires the expected or unexpected response.

In the later ERP components, there were a number of findings that speak to the processes underlying how postspotlight masking may arise when a location expectancy is combined with a response expectancy. First, the P2 occurred earlier for targets at the expected location, relative to the targets presented at the unexpected location. This result suggests that spatial selection served to expedite P2-related processing, an affect on attended-location targets that was independent of the response expectancy associated with the target. Accordingly, the P2 data thus provide compelling support for the position that the high error rate for unexpected targets at the expected location may be mediated in part by an attention-related speeding of the target processing sequence, as discussed above.

Second, the N2 latency data provide the earliest evidence of when the processing of spatially selected targets begins to vary as a function of response expectancy. In particular, the peak latency

of the N2 was significantly earlier for the expected targets at the expected location, relative to all other target expectancy combinations. This effect is clearly seen in the ERP difference wave in Figure 4a, where the waveform does not diverge significantly from baseline until just after 200 ms poststimulus. The sensitivity of the N2 to response expectancy at the attended location is also seen in the amplitude data, where the N2 had a greater negativity for targets of the unexpected orientation, relative to targets of the expected orientation (see Table 7 later on). Given that the N2 is typically more negative for low-probability events (see Coles & Rugg, 1995; Näätänen, 1992), the N2 data here thus provide direct evidence that participants had generated an expectancy for targets of the cued orientation and that the mismatch between the expected and the presented target was manifest at the attended location no later than the N2 latency range. In comparison, processing of targets at the unexpected location did not show prominent evidence of diverging on the basis of orientation expectancy until the P300 time range (Figure 4b).

Finally, although the N2 showed a sensitivity to orientation expectancy that was location dependent, the P300—which, like the N2, shows an increase in amplitude for low-probability events (see Coles & Rugg, 1995; Näätänen, 1992)—showed a sensitivity to orientation expectancy that was not location specific. In partic-

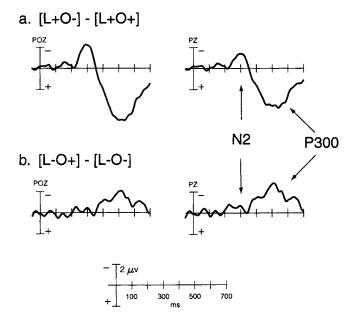


Figure 4. The ERP difference waves for orientation-specific processing in the central parietal event-related potential (ERP) components as a function of location, from electrodes POZ and PZ. (a) This difference wave highlights the latency of the N2 at which targets at the expected location are dissociated on the basis of whether they were of the expected or unexpected orientation. The wave shown was produced by subtracting the L+O+ trace in Figure 3 from the L+O- trace. (b) This ERP difference wave shows the latency of when the N2 for targets at the unexpected location begins to dissociate between targets of the expected and unexpected orientation. The important point here is that this occurs at a later latency than for targets at the expected location, as seen in Figure 4a. The wave shown was produced by subtracting the L-O+ trace in Figure 3 from the L-O- trace. L+ = location cued; L- = location uncued; O+ = orientation cued; O- = orientation uncued.

ular, the P300 was prominent for targets of the unexpected orientation, as can be seen in the ERP difference wave in Figure 5a. The P300 data thus reveal two important aspects of the processing operations underlying combined location and response expectancies. First, like the N2, the P300 data confirm that participants were generating an expectancy for the cued-target orientation, given that the P300 is larger for low-probability stimuli. Second, the data demonstrate that orientation-specific processing (Figure 5a) occurred after location-specific processing (Figure 5b) had been completed. We relate all of these findings to models of postspotlight masking in the General Discussion.

General Discussion

Behavioral researchers have debated whether combining a location expectancy with either a form or a response expectancy leads to failure or masking of the attentional spotlight (e.g., Kingstone, 1992; Klein, 1980, 1994; Klein & Hansen, 1987, 1990; Lambert, 1987; Lambert & Hockey, 1986). In Experiment 1, we replicated the characteristic data pattern underlying this debate by combining location and response expectancies: RTs were longer and error rates were higher to targets of the unexpected orientation at the expected location, relative to targets of the expected orientation at the expected location. In Experiment 2, the early ERP components revealed that despite this reliable difference in behavioral performance, initial processing in visual cortex was equiva-

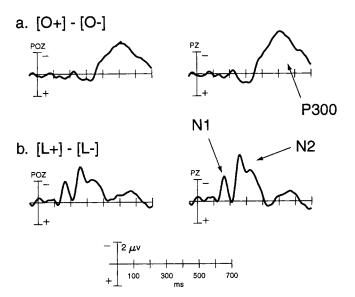


Figure 5. The event-related potential (ERP) difference waves for orientation- and location-specific processing in the central parietal ERP components, from electrodes POZ and PZ. (a) This difference wave highlights the prominence of the P300 for targets of the unexpected orientation, relative to the expected orientation, collapsed for target location. The wave shown was produced by subtracting the collapsed O+ traces from Figure 3 from the collapsed O- traces. (b) This difference wave highlights the prominent N1 and N2 for targets at the expected location, relative to targets at the unexpected locations. The wave shown was produced by subtracting the collapsed L- traces from Figure 3 from the collapsed L+ traces. L+ = location cued; L- = location uncued; O+ = orientation cued; O- = orientation uncued.

lent for targets of the expected and unexpected orientation at the expected location. These results thus provide direct electrophysiological evidence that combined spatial and response expectancies do not lead to a failure of the attentional spotlight. Rather, the data suggest that there is initial processing facilitation for all targets at the attended location, but this facilitation is selectively obscured or masked for the unexpected targets at the attended location by subsequent decision- and response-related processing. In the following sections, we examine the implications and issues that arise from these findings.

Postspotlight Masking

Given that the early ERP components suggest that the initial facilitatory effects of spatial attention for all targets at the expected location are being masked by subsequent processing events, what do the later ERP components reveal about this postspotlight masking? This question concerns identifying when and where processing operations diverge for expected and unexpected targets at the expected (or attended) location. Such evidence was found in the N2 component, and in regard to postspotlight masking, the N2 showed two important patterns for targets presented at the attended location. First, the latency of the N2 peak was earlier for targets of the expected orientation, in comparison to targets of the unexpected orientation. Second, the amplitude of the N2 was larger (i.e., was more negative) for targets of the unexpected orientation, relative to targets of the expected orientation. Although it remains an open question whether these latency and amplitude differences reflect common or different processing events, the critical point here is that processing for attended-location targets was first observed to diverge on the basis of the response expectancy in the latency range of the N2. In contrast, for targets presented at the unexpected location, there was little apparent distinction being made between targets of the expected and unexpected orientation within the N2 latency range, as highlighted in Figure 4. The data thus suggest that the processing indexed by the N2 is a strong candidate for contributing to the postspotlight masking effect generated by the response expectancy.

A related enigma of the combined expectancy phenomenon has been the increased error rate for unexpected targets at the attended location. One explanation for this accuracy effect is that on the basis of the response expectancy, there is a bias to categorize targets at the attended location as having the expected orientation (e.g., Klein & Hansen, 1990). The N2 and P300 data are not inconsistent with this proposal, given that both components are known to be sensitive to low-probability stimulus events (e.g., Coles & Rugg, 1995; Näätänen, 1992). In particular, the N2 amplitude was enhanced for unexpected targets at the attended location, and the P300 was enhanced for all targets of the unexpected orientation. These data thus indicate that participants were expecting targets of the cued-target orientation, which had the higher presentation probability. How a response expectancy may be similar to or different from categorization remains unclear, but the N2 data do suggest the possible ERP correlates of where the error-related effects are selectively occurring for targets of the unexpected orientation at the attended location.

Taken together, the ERP data thus converge on the following model of how response expectancy interacts with location expectancy. Initially, spatial selection speeds the processing of all stim-

uli at the attended location, as suggested by the shift in P2 latency as a function of target location. The relative slowing of unexpected targets at the attended location and the associated increase in error rate then arise subsequent to this P2 effect, as suggested by the N2 data. At the cognitive level, the most likely explanation for this postspotlight masking effect would be that participants are required to reprogram the correct response for those targets that had the unexpected orientation, a process that would necessarily delay responses relative to when targets had the expected orientation. In turn, the increased error rate may reflect a difficulty in withholding the expected response, a problem potentially confounded by the speeded time course of processing for all targets at the attended location. As a result, the comparable RTs for all targets of the unexpected orientation may possibly reflect the costs of reprogramming the correct response, whereas the error rates for these targets may differ as function of location because only at the attended location were processing events speeded. In contrast, the RTs for expected targets show the normal pattern of shorter RTs for stimuli at attended locations in comparison to unattended locations because there was no required motor reprogramming. In this scenario the RT benefits afforded by spatial attention to the unexpected targets at the attended location are absorbed into the slack time generated during response reprogramming (see Johnston, McCann, & Remington, 1995, 1996).

The notion that responses are delayed to unexpected targets at the expected location because of motor reprogramming suggests that participants may show evidence of preparing the cued response during the cue-target interval. In our study, cuing the expected form of the target also cued the most likely hand that would be required to make the response to the target. As a result, this design allowed us to make a post hoc examination of motor preparation activity in the cue-target interval, on the basis of the lateralized readiness potential (LRP). The LRP is an ERP derived from measurements at lateralized central scalp electrodes that overly motor cortex. Typically, when a participant is preparing to respond with a hand, central electrode sites contralateral to the prepared hand become more negative relative to the ipsilateral electrode sites (e.g., Gehring, Gratton, Coles, & Donchin, 1992). Presumably, this negativity reflects the lateralized activation of motor cortex for the hand that is being prepared to make the upcoming response (see Coles, 1989). Accordingly, if participants in our study were preparing to respond with their cued hand prior to target onset, a lateralized negativity should be evident at electrode sites contralateral to the cued hand. If so, this result would lend strong support to the motor reprogramming hypothesis because such a pattern would imply that cuing led to a response activation.

Two different analyses based on the LRP were performed. First, the data for 5 participants in Experiment 2 were reaveraged to time-lock to the onset of the cue. The data for lateral central electrode sites C3 and C4 were then examined as a function of whether a left-handed or right-handed response was cued. These data revealed little evidence of a negativity—lateralized or not—in the 1,000-ms following cue onset, possibly because of a cue—target interval that was randomly jittered between 600 and 800 ms and that may have smeared out any pretarget negativity. Accordingly, a second analysis was performed on these same 5 participants that was based on time-locking to the onset of the target and looking backward in time into the cue—target interval to see if a negativity

had developed just prior to target onset. Using a baseline measure of -600 to -800 ms pretarget (which placed the baseline in the approximate time of cue onset), this analysis revealed that a negativity had in fact developed at C3 and C4. However, there was no systematic lateralization in the negativity, suggesting that participants may not have been preferentially activating motor cortex associated with the cued hand. The data from the centrolateral electrode sites thus do not support the idea that motor responses were primed by the cue information. Instead, the data are consistent with two alternative possibilities: (a) The failure to observe a cuing effect for unexpected targets at the expected location may be mediated—either partly or wholly—by attentional priming of orientation-related processing, or (b) if motor reprogramming is indeed underlying the delayed responses to unexpected targets at the expected location, then the effect may not be associated with lateralized activation of motor cortex.

Response Versus Form Expectancies

Another question stemming from this study concerns whether the pattern of ERP results would differ if response expectancy was uncoupled from form expectancy, as has been done previously in behavioral studies (e.g., Kingstone, 1992; Lambert, 1987; Lambert & Hockey, 1986). In terms of the spotlight failure versus postspotlight masking debate, it is unlikely that combining a location expectancy with a pure form expectancy would produce failure instead of masking. The reasons for this are two-fold. First, the cortical generators of the lateral occipital P1 and N1 components, which show evidence of the initial spotlight facilitation, have been localized to extrastriate visual cortex (e.g., Clark & Hillyard, 1996; Heinze et al., 1994; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997). Given that form information is processed in temporal cortical areas that ultimately receive their input from the earlier extrastriate areas mediating spatial selection (e.g., Desimone & Ungerleider, 1989; Felleman & Van Essen, 1991), any model suggesting that form expectancies should lead to selective failure of the preceding spatial processing operations would be faced with accounting for these anatomical constraints.

Second, the time course of processing events associated with spotlight masking described above closely parallels the results from ERP studies investigating hierarchical feature selection (e.g., Anllo-Vento & Hillyard, 1996; Hillyard & Münte, 1984; Smid, Jakob, & Heinze, 1997). For example, Eimer (1995a) examined the ERP correlates of transient attentional shifts to the location and color of potential target stimuli. On each trial, participants were cued for both a location and a color, and if the subsequent stimulus matched both the location and color indicated by the cue, a simple go response was then required. Consistent with a spotlight effect, the N1 reported by Eimer (1995a) showed a larger amplitude for stimuli at the cued versus uncued location, independent of stimulus color. Further, relative to stimuli with an uncued color, stimuli of the cued color showed a broad negativity in a comparable time range to our N2, a negativity that was even larger when the stimulus was at the attended location. As a result, whether combined expectancy or hierarchical processing tasks are used, in both

⁵ Only 5 of the 8 participants' data were reaveraged due to corruption of the raw data storage medium for 3 of the participants.

cases clear electrophysiological evidence is found suggesting that initial selection is based solely on spatial location, with effects on processing from other stimulus attributes arising only at subsequent processing stages.

Instead, uncoupling form and response expectancies would likely alter the pattern of postspotlight processing events relative to what was observed here. Indeed, looking at a pure form expectancy in conjunction with a location expectancy would be an effective manner in which to begin disentangling what postspotlight processing operations are associated with which later ERP patterns, in terms of form- and response-based effects. For example, if unexpected responses result in slack time for response reprogramming as suggested above, this result would presumably not arise if a form expectancy was used that did not include response-based contingencies as well. Consistent with this possibility, when Kingstone combined location and form expectancies in a behavioral study (1992, Experiments 1 and 2), not only was the strength of spotlight masking weakened relative to combined location/response expectancies (see introduction and Footnote 1), but the error rate was not significantly higher for unexpected forms at the expected location. Taken collectively, the data thus suggest that postspotlight masking may have multiple causes and neural loci—depending on the nature of the nonspatial expectancies involved. The next step is to begin investigating such differences using both electrophysiological and hemodynamic measures of cortical function.

Stimulus-Response Compatibility

A final topic that must be addressed centers on stimulusresponse (S-R) compatibilities and how they may have biased participants' expectancies and their RTs to the targets. It has long been known that RTs to lateralized targets are shorter if the response to the target is made with the hand on the same side of visual space as the target (e.g., Simon, 1969). Given that in the current study participants used separate thumbs to signal the orientation of the target raises the concern that RTs may have been influenced by this phenomenon, known as the Simon effect. To investigate this possibility more closely, we reexamined the behavioral data from both experiments in relation to whether the hand of response was on the same or opposite side of space as the target stimulus. Collapsing the data across the two experiments to increase statistical power, we performed an ANOVA on the RT data with factors of orientation expectancy, location expectancy, and hand of response (same vs. opposite side of target). This omnibus ANOVA showed no overall three-way interaction (p >.25), nor an interaction between hand and location (p > .9). However, there was a main effect of hand (p = .072), and an interaction between hand and orientation (p = .069) that approached significance. Using two-tailed t tests to make comparisons between hand of response within each expectancy condition revealed a significant Simon effect for targets of the expected orientation at both the expected (p < .005) and unexpected (p < .005) .05) locations but no comparable effects for targets of the unexpected orientation at either location (ps > .18).

That the Simon effect arose when the expected response was made but was reduced or eliminated by the unexpected response is consistent with the position that responses are delayed for all targets of the unexpected orientation because of the reprogramming of the correct (i.e., unexpected) response. In other words, nonspatial response expectancies may be interacting with-and disrupting—the spatial representations presumably associated with the Simon effect. For example, a recent ERP study of S-R compatibilities by Eimer (1995b) reported that within 200 ms of the onset of an arrow that cues the most probable location of an impending target, automatic activation of response-related processing occurs for the hand on the cued side of space. Importantly, however, this automatic activation decayed and was followed by a second response-related activation phase—beginning within the same time range as our cue-target stimulus onset asynchronythat was reflective of the specific response contingencies associated with the task. Our data are consistent with this notion, where the Simon effect is maintained if the expected response is to be made by the hand on the expected side of space, but the effect is reduced or eliminated when the expected response is incongruent with the automatic activation reported by Eimer (1995b).6

Conclusions

The ERP data presented here provide direct electrophysiological evidence demonstrating that combined location and response expectancies lead to masking of the spotlight of spatial attention, not to spotlight failure. That is, although attention can take many forms in processing (e.g., Desimone & Duncan, 1995), when locational expectancies are associated with an impending target stimulus, early selection will take the form of a spatial spotlight even when other stimulus expectancies are concurrently generated. One of the interesting outcomes of this study is that in affirming the central role of spatial selection in the combined expectancy phenomenon, the data speak as well to the consequences of spatial selection. That is, ERP studies have long focused on establishing that spatial selection within extrastriate cortex leads to sensory gain for stimuli in attended spatial locations (e.g., Luck et al., 1994; Mangun, Hansen, & Hillyard, 1987; Van Voorhis & Hillyard, 1977). The broader implications of the current study are that we can now begin to examine what this sensory gain affords in terms of postperceptual processing. The results presented here suggest that one outcome may be to expedite the processing for spatially selected stimuli, where stimulus attributes at the attended location are resolved more quickly relative to stimulus attributes in unattended spatial locations. Uncovering how such effects vary as a function of nonspatial stimulus expectancies represents the next generation of questions to be examined in combined expectancy studies.

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⁶ It has been hypothesized that the response activation associated with lateralized stimuli that drives the Simon effect rapidly decays after stimulus onset (e.g., De Jong, Liang, & Lauber, 1994; Hommel, 1993). Because responses to targets requiring the unexpected response were longer relative to the responses made for targets requiring the expected response, the decay hypothesis provides another plausible explanation for why no Simon effect was observed when targets required the unexpected response.

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Received April 14, 1999
Revision received May 30, 2000
Accepted June 2, 2000 ■

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