Pushing around the Locus of Selection: Evidence for the Flexible-selection Hypothesis

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Abstract

■ Attention operates at an early stage in some experimental paradigms and at a late stage in others, which suggests that the locus of selection is flexible. The present study was designed to determine whether the locus of selection can vary flexibly within a single experimental paradigm as a function of relatively modest variations in stimulus and task parameters. In the first experiment, a new method for assessing the locus of selection was developed. Specifically, attention can influence perceptual encoding only if it is directed to the target before a perceptual representation of the target has been formed, whereas attention can influence postperceptual processes even if attention is cued after perception is complete. Event-related potentials were used to confirm the validity of this method. The subsequent experiments used cueing tasks in which subjects were required to perceive and remember a set of objects, and the difficulty of the perception and memory components of the task were varied. When the task overloaded perception but not working memory, attention influenced the formation of perceptual representations but not the storage of these representations in memory; when the task overloaded working memory but not perception, attention influenced the transfer of perceptual representations into memory but not the formation of the perceptual representations. Thus, attention operates to select relevant information at whatever stage or stages of processing are overloaded by a particular stimulus–task combination. ■

INTRODUCTION

In the early days of research on selective attention, investigators debated whether attention operates at an early stage—influencing the formation of perceptual representations—or at a late stage—influencing which perceptual representations were available for overt report and for storage in memory (see review by Luck & Vecera, 2002). This locus-of-selection debate has continued for many years. In this article, we describe an alternative to the traditional early-selection and late-selection positions that we call "flexible selection," in which the locus of selection varies according to the nature of the stimuli and task.

Over the past 20 years, several experiments have been published that provide convincing evidence that attention operates at an early stage under certain conditions. For example, conventional cognitive experiments have demonstrated that attention can influence the detection of simple luminance increments (Luck, Hillyard, Mouloua, Woldorff, et al., 1994) and that the effects of attention interact with stimulus quality (Pashler, 1984). Psychophysical studies have also shown that attention increases contrast sensitivity and spatial resolution, altering the appearance of stimuli (Carrasco, Ling, & Read, 2004; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Yeshurun & Carrasco, 1998). In addition, electrophysiological studies have shown that attended stimuli elicit larger sensory responses than ignored stimuli. Event-related potential (ERP) studies have demonstrated that the sensory-evoked P1 wave is larger for attended stimuli than for ignored stimuli (see reviews by Hillyard, Vogel, & Luck, 1998; Mangun, 1995). This effect typically begins within 100 msec of stimulus onset and has been localized to extrastriate areas of the visual cortex (Di Russo, Martinez, & Hillyard, 2003; Heinze, Mangun, et al., 1994). Sensory modulations have also been demonstrated in single-unit recordings from macaque monkeys (Luck, Chelazzi, Hillyard, & Desimone, 1997; Treue & Maunsell, 1995; Motter, 1993). For example, sensory responses in area V4—an intermediate stage in the ventral visual processing pathway—were found to be enhanced for attended stimuli compared to ignored stimuli beginning at 60 msec poststimulus, which is the onset time of the sensory response in that area (Luck, Chelazzi, et al., 1997). Neuroimaging studies have also shown that attention influences neural activity in the visual cortex (see review by Kastner & Ungerleider, 2000) and even in the lateral geniculate nucleus (O'Connor, Fukui, Pinsk, & Kastner, 2002). These results suggest that attention can influence the gain of feedforward sensory transmission (for a review, see Hillyard et al., 1998).

These compelling demonstrations of early selection do not imply that attention always (or even frequently)

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operates at the level of perception.[1] Indeed, there have been several compelling demonstrations in recent years that attention operates to influence postperceptual processing in certain experimental paradigms, with no influence on perception. Perhaps the best example of this is the ''attentional blink'' paradigm, in which each trial consists of a rapid serial visual presentation stream of foveally presented stimuli, two of which are targets that must be reported at the end of the trial. Accuracy for the second target is found to be impaired when it appears within approximately 500 msec of the first target, as if processing the first target led to a ''blink'' of attention during which the second target was missed (see review by Shapiro & Luck, 1999). The study that pioneered the prototypical attentional blink paradigm proposed that the impaired performance for the second target is caused by a failure of perception (Raymond, Shapiro, & Arnell, 1992). However, subsequent behavioral and ERP studies demonstrated unequivocally that the second target is perceived even though it cannot be accurately reported (e.g., Vogel, Luck, & Shapiro, 1998; Shapiro, Driver, Ward, & Sorensen, 1997). Rather than reflecting impaired perception, the attentional blink appears to occur because a fully formed perceptual representation of the second target is overwritten by the next item in the stream before it can be consolidated in working memory (Vogel & Luck, 2002; Giesbrecht & Di Lollo, 1998). This has become a widely accepted case of postperceptual selection.

Although attention has been observed to operate in different cognitive and neural systems for different tasks, these observations do not necessarily indicate that the locus of selection is truly flexible. In particular, the tasks used to show different loci of selection differ along a wide variety of dimensions, and it is not always clear that the term *attention* even means the same thing in these different paradigms. For example, observers in a spatial cueing experiment are explicitly encouraged to pay more attention to the cued location than to the uncued location, whereas observers in an attentional blink experiment are attempting to encode two targets at the same location and fail to encode the second target despite their best efforts. To understand the factors that control the locus of selection, it is important to be able to systematically vary the locus of selection within a single experimental paradigm.

Lavie and Cox (1997) and Lavie (1995) have developed an approach for manipulating the locus of selection within a single task in the context of their ''perceptual load hypothesis.'' This hypothesis states that perceptual processing systems have a certain amount of processing resources, and all available resources are always devoted to processing sensory inputs. If the available resources are insufficient to process all of the inputs, then attentional processes may be used to allocate more resources to some inputs and fewer resources to other inputs. If the system is not overloaded, however, then all inputs will be processed automatically, regardless of any intentions to attend more to some inputs than to others. To test this hypothesis, the degree of perceptual load was varied in the Eriksen flankers task. The general finding from these experiments is that less interference is observed from the flankers when the perceptual load is higher, which suggests that selection occurs at a late stage under low-load conditions but shifts to an early stage under high-load conditions.

However, this conclusion assumes that a lack of response-level interference implies perceptual suppression of the distractors, which may not be a valid assumption. The elimination of distractor interference could instead be explained by an increase in the effectiveness of selection within an intermediate stage of processing (e.g., a stage that follows object identification but precedes response selection) or within the response selection system itself. Thus, although the finding of load-dependent changes in interference is consistent with the idea of flexible selection, it is important to provide converging evidence. Stronger evidence for a shift in the locus of selection in this paradigm has been provided by ERP and neuroimaging studies of distractor processing, which have provided evidence that the perceptual processing of distractors is suppressed when the cognitive load is increased (Handy, Solotani, & Mangun, 2001; Rees, Frith, & Lavie, 1997). The present study provides additional converging behavioral and ERP evidence using a very different approach.

Experiment 1 develops a new method of manipulating the locus of selection, using ERPs to provide evidence that attention influences the formation of perceptual representations under some conditions and that only postperceptual processes are influenced under other conditions. This approach is then used in Experiments 2–4 to demonstrate that attention influences the formation of perceptual representations under conditions of high perceptual load and influences the formation of working memory representations under conditions of high memory load.

EXPERIMENT 1

The goal of Experiment 1 was to provide a new method for manipulating the locus of selection. Our approach was based on varying the cue–target stimulus onset asynchrony (SOA) in the spatial cueing paradigm, as illustrated in Figure 1. Logically, attention cannot influence the formation of a perceptual representation unless it has shifted before the perceptual representation has been formed. Consequently, cue-triggered shifts of attention can influence the formation of a perceptual representation only if the cue is presented prior to the onset of the to-be-perceived information.[2] Indeed, many previous studies have demonstrated that spatial cues are ineffective unless they precede the target by a sufficient period (e.g., Luck, Hillyard, Mouloua, & Hawkins,

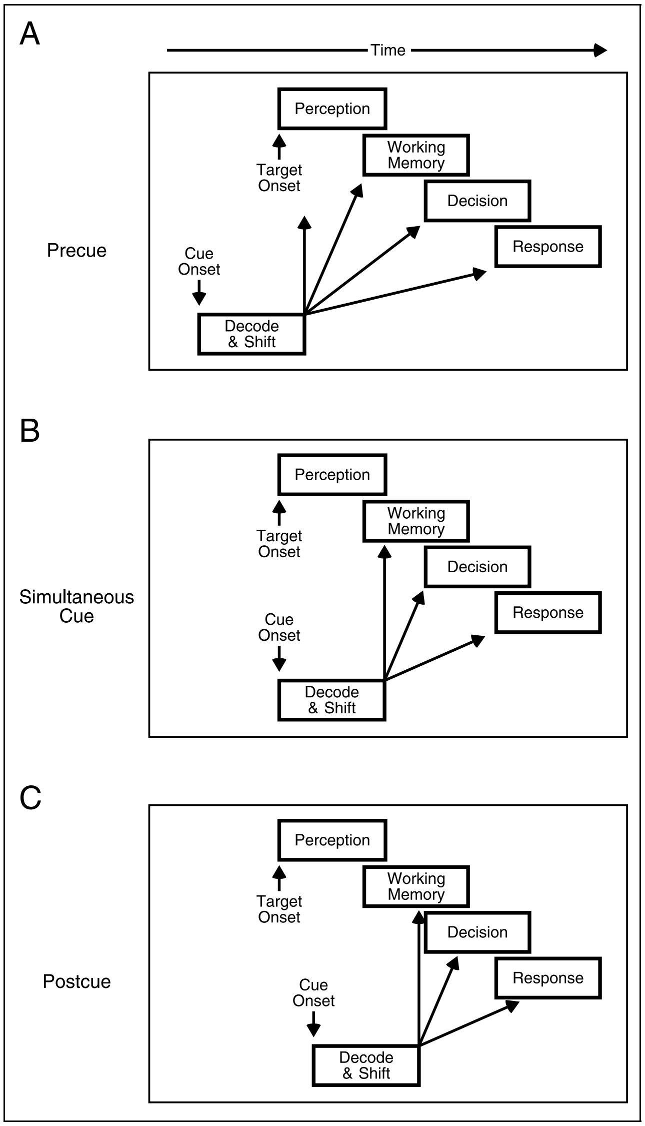

Figure 1. Relationship between cue–target delay interval and the stages of processing that can potentially be influenced by cue-directed attention. (A) When the cue precedes the target by a significant interval, attention can be shifted before the perceptual representation of the target has been formed. (B) When the cue and target are simultaneous, perceptual analysis of the target will typically be complete before attention has been shifted, so attention cannot influence perception (but can influence postperceptual processes). (C) When the cue appears after the target, it is even less likely that attention can influence the perception of the target; however, postperceptual processes can still be influenced by attention if the perceptual representation of the target has not completely faded before attention is shifted.

1996; Cheal & Lyon, 1991; Posner, 1980). More specifically, to influence perception, a cue must precede the target by enough time for the cue to be decoded and for a shift of attention to be programmed and executed before a perceptual representation of the target has been formed (as in Figure 1A).

In contrast, it is sometimes possible for postperceptual processes to be influenced by attention even if the cue is simultaneous with or follows the target information. In fact, this is the basis for the classic iconic memory experiments of Averbach and Coriel (1961) and Sperling (1960). In these experiments, an array of alphanumeric characters was presented, and a cue was presented at some time before or after the array, indicating that a particular subset of the array should be remembered. The cues were found to be effective even when presented after the offset of the stimulus array, as long as perceptual information about the stimulus array (i.e., iconic memory) had not yet decayed. In essence, the cues allowed the observers to selectively transfer a subset of the perceptual information into working memory.

Thus, it should be possible to manipulate the locus of selection by varying the cue–target SOA. When the cue is simultaneous with the target (or follows it), only late-selection mechanisms should influence performance; when the cue precedes the target by a sufficient period of time, both early- and late-selection mechanisms can potentially influence performance. This parallels the approach used by Lavie and her colleagues, in which low-load tasks lead only to late selection but high-load tasks lead to both early and late selection.

Experiment 1 was designed to provide a direct test of this new method for manipulating the locus of selection. The experiment used a task in which precues or simultaneous cues were used to indicate which one of four potential target locations should be attended. The stimuli and task were designed so that both perceptual and postperceptual processes would be overloaded. We predicted that precues would influence both the formation of perceptual representations and the transfer of these representations into working memory; in contrast, simultaneous cues should be too late to influence the formation of the perceptual representations but could still influence the transfer of these representations into working memory. We therefore expected accuracy to be higher on valid trials than on invalid trials in both conditions, but we also expected that this effect would be larger for precues because they have the advantage of influencing both perception and working memory.

Although this pattern of behavioral results would be consistent with the addition of an early-selection mechanism for precue trials, it would not provide direct evidence that precues influence the perception of the target whereas simultaneous cues do not. The methodological challenge of this experiment was therefore to directly determine whether the cues influenced the formation of a perceptual representation of the target. To solve this problem, we used an approach that we previously developed for assessing the locus of selection in the attentional blink paradigm (Vogel, Luck, et al., 1998). Specifically, we recorded ERPs and focused on the N400 component, a portion of the ERP waveform that is highly sensitive to semantic mismatch (Kutas & Federmeier, 2000). For example, when observers are shown sentences one word at a time, the last word of the sentence "He brushed his teeth and combed his bus" would yield a much larger N400 than the last word of the sentence "He brushed his teeth and combed his hair." The same effect can also be observed with simple pairs of sequentially presented words, an initial word that establishes a semantic context and a second word that either does or does not violate this context. For example, when "garden" is presented as the context word, the subsequent presentation of "suitcase" would elicit a large N400, but the subsequent presentation of "vegetable" would not.

The N400 component can be used to assess the locus of selection using the following logic. A semantically mismatching word will elicit a larger N400 than a semantically matching word, but this is possible only if the word has been identified. Thus, the presence of a large N400 for an ignored mismatching word indicates that this word was identified to the point of making contact with semantic information. More precisely, if the difference in N400 amplitude between mismatching and matching trials is the same for attended and ignored words, then the ignored words must have been accurately identified. In the attentional blink paradigm, for example, the second target is perceived and generates a large N400 even though it cannot be accurately reported (Vogel, Luck, et al., 1998).

The design of the present experiment is illustrated in Figure 2. Each trial began with the presentation of a "context word" that was used to establish a semantic context for that trial. This was followed by an array containing a target word and three consonant strings that served as distractors, and this array was followed by a set of masks. The subject's task was to indicate, by means of an unspeeded button press, whether the target word was semantically related or unrelated to the context word. The N400 could therefore be isolated by forming difference waves in which the waveform elicited by related targets was subtracted from the waveform elicited by unrelated targets. This difference reflects the brain's differential processing of related and unrelated words, and a nonzero difference indicates that the words were identified to the point of semantic analysis.

Attention was manipulated by means of a central arrow cue that indicated the likely location of the target word (cue validity = 75%). This cue appeared either 2000 msec before the target array (precue condition) or simultaneously with the target array. A very long cue–target delay interval was used in the precue condition to ensure that the ERP response elicited by the cue would end before the onset of the ERP response elicited by the target array.

This task was designed to be demanding for both perceptual and postperceptual processes. Perception was overloaded by the simultaneous presentation of four potential target strings; thus, performance could be improved by focusing perceptual processing onto the cued location. Working memory encoding was overloaded because the masks could overwrite the perceptual representations before they could be transferred into working memory. We have previously demonstrated that, with somewhat different stimuli, the process of transforming a perceptual representation into a durable working memory representation (called *short-term consolidation* or *vulcanization*) is capacity-limited and requires approximately 50 msec per object (Vogel, Woodman, & Luck, in press). Thus, performance could

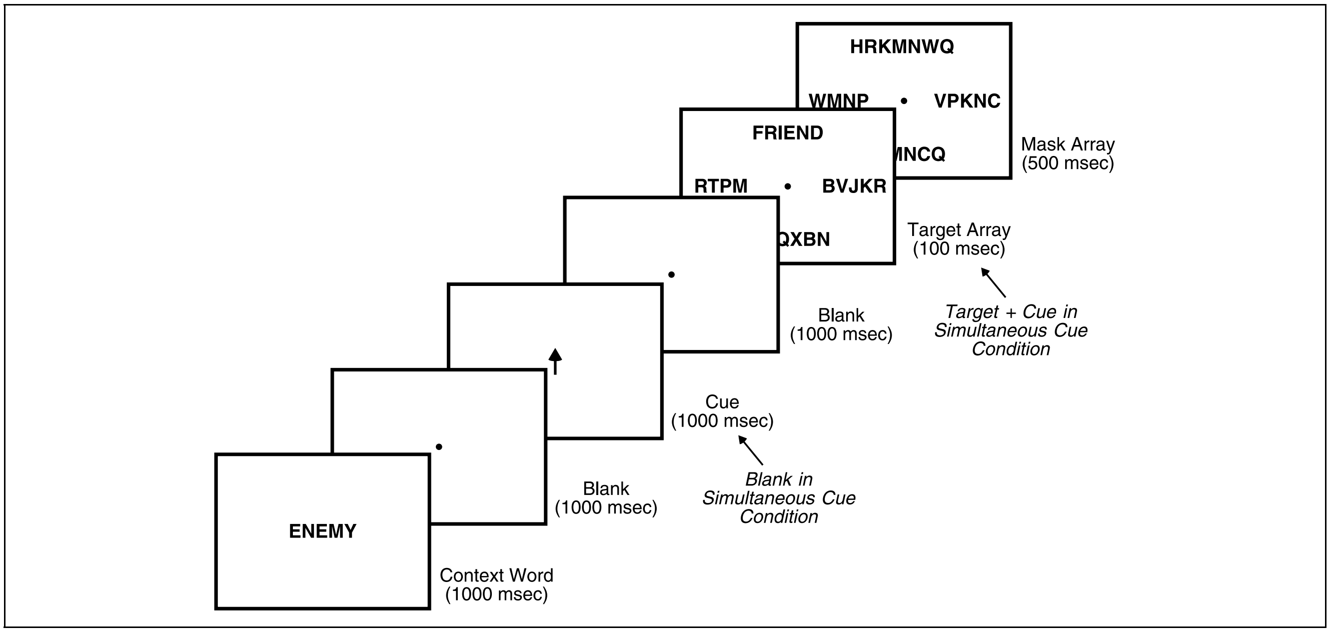

Figure 2. Example of a valid precue trial in Experiment 1.

be improved by focusing this process onto the perceptual representation at the cued location.[3]

Our predictions were as follows. First, consider the precue condition. In this condition, we predicted that behavioral performance would be highly accurate on valid trials because attention would enhance both the formation of a perceptual representation of the target and the transformation of this perceptual representation into a durable working memory representation that could survive the presentation of the masks. Similarly, because of the accurate perceptual encoding of the target on valid trials, we predicted a large difference in N400 amplitude between validly cued target words that matched versus mismatched the context word. On invalid trials, behavioral performance was expected to be inaccurate because the target would receive impaired perceptual processing, and whatever perceptual representation was formed would likely be masked before it was transformed into a durable working memory representation. The impaired perception was also expected to yield a reduced N400 difference between targets that matched versus mismatched the context word.

Now consider the simultaneous cue condition. On valid trials, attention will be shifted too late to enhance the target's perceptual representation. However, the perceptual task was only moderately difficult, so the observers should be able to form a moderately accurate perceptual representation of the target without the benefit of spatially focused attention. Moreover, the transfer of this moderately accurate representation into working memory should be enhanced by attention on valid trials. Thus, performance on valid trials should be fairly accurate in the simultaneous cue condition, but it should be somewhat less accurate than performance on valid trials in the precue condition. The less accurate perceptual representations should also decrease the size of the N400 difference between semantically related and unrelated valid targets in the simultaneous cue condition compared to the precue condition.

On invalid trials in the simultaneous cue condition, the perceptual representation of the target should be equivalent to the perceptual representations on valid trials. However, the perceptual representations on invalid trials will not be efficiently transferred into working memory, so the perceptual representations will have little opportunity to influence behavioral accuracy and performance should be poor. The accurate perceptual representation should, however, make it possible for subjects to perform a semantic comparison between the target and the context word, and the N400 difference between semantically related and unrelated targets should be just as large for invalidly cued targets as for validly cued targets. Thus, we predicted that cue validity would influence behavioral performance in both the precue and simultaneous cue conditions but that N400 amplitude would be suppressed on invalid trials only in the precue condition.

Results

Behavioral Data

The behavioral results are summarized in Figure 3A. Accuracy was collapsed across semantically related and unrelated trials and analyzed in an ANOVA with factors of cue timing and cue validity. Accuracy was greater for valid trials than for invalid trials, leading to a significant main effect of cue validity [$F(1,19) = 74.25$, $p < .001$]. The validity effect was present for both conditions but, as predicted, was somewhat larger in the precue condition than in the simultaneous cue condition, leading to a significant interaction between cue

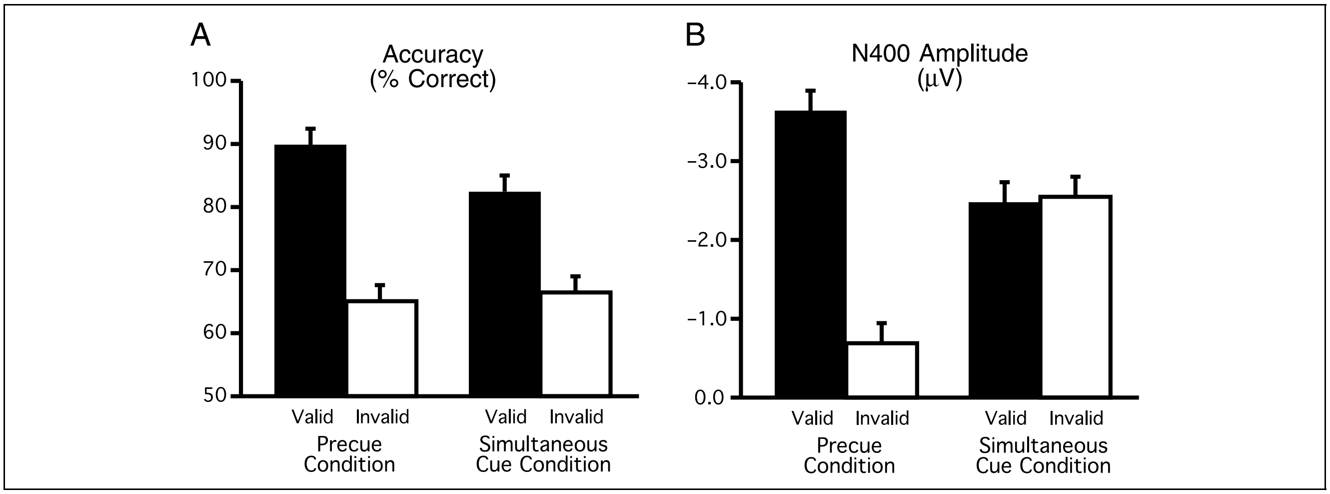

Figure 3. Mean accuracy (A) and mean N400 amplitude (B) for valid and invalid trials with precues and simultaneous cues in Experiment 1. N400 amplitude was measured from the unrelated-minus-related difference waves and averaged across all nine frontal, central, and parietal electrode sites. Error bars in this figure and the following figures show 95% within-subjects confidence intervals.

validity and cue timing [$F(1,19) = 10.24, p < .005$]. This was primarily due to greater accuracy on valid trials in the precue condition than in the simultaneous cue condition.

Planned follow-up analyses yielded significant cue validity effects in both conditions ($p < .001$). In addition, because we predicted that performance would be more accurate for valid trials in the precue condition than in the simultaneous cue condition, we conducted a planned comparison of these two cells. This analysis indicated that performance on valid trials was indeed significantly more accurate in the precue condition than in the simultaneous cue condition ($p < .001$). When invalid trials were compared in this manner, however, the difference between the precue and simultaneous cue conditions was not significant ($F < 1$). These results are consistent with the hypothesis that attention influenced both perceptual and postperceptual processes in the precue condition but influenced only postperceptual processes in the simultaneous cue condition.

ERP Data

The ERP data are summarized in Figure 4, which overlays the waveforms elicited by targets that were semantically related and semantically unrelated to the context word. Figure 5 shows difference waves that isolated the N400 component by subtracting the related-target waveforms from the unrelated-target waveforms, and mean N400 amplitude measured from these difference waves is summarized in Figure 3B.

The N400 amplitudes measured from the difference waves were analyzed in a within-subjects ANOVA with factors of cue timing, cue validity, anterior–posterior electrode position (frontal, central, parietal), and left–right electrode position (left hemisphere, midline, right hemisphere). Overall, the N400 was larger at central and

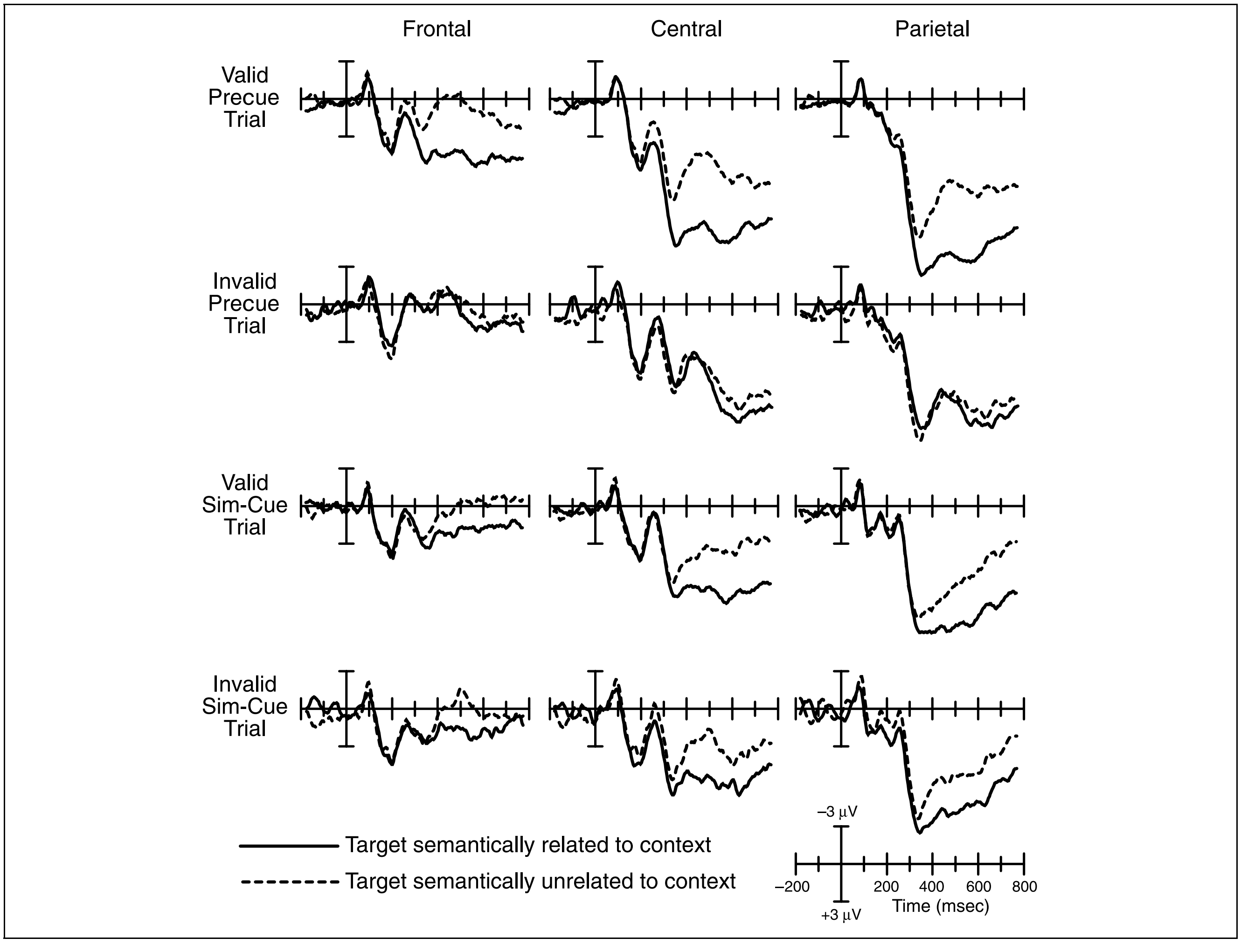

Figure 4. Grand-average ERPs elicited by the target stimuli at frontal, central, and parietal midline electrode sites in Experiment 1. The waveforms for related and unrelated targets are overlaid, presented separately for valid and invalid trials in the precue and simultaneous cue (*Sim-Cue*) conditions. Negative is plotted upwards. The waveforms in this and the following figure were low-pass filtered by convolving them with a Gaussian impulse–response function (full width at half maximum = 14 msec; half amplitude cutoff = 30 Hz).

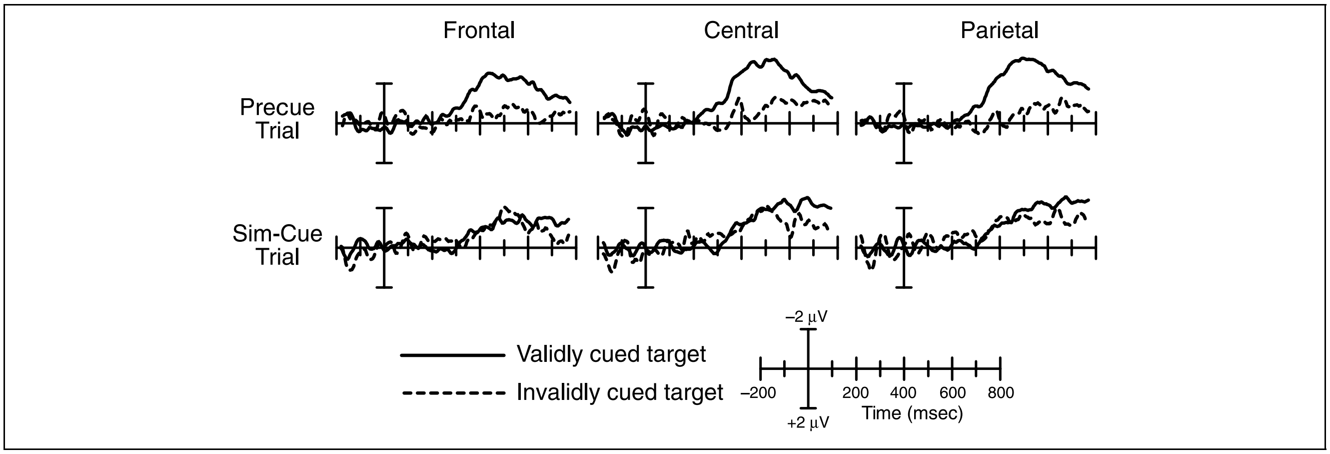

Figure 5. Grand-average ERP difference waveforms created by subtracting the waveform elicited by semantically related targets from the waveform elicited by semantically unrelated targets. The waveforms are presented separately for valid and invalid trials in the precue and simultaneous cue (*Sim-Cue*) conditions. Negative is plotted upwards.

parietal electrodes than at frontal electrodes, was larger at midline electrodes than at lateral electrodes, and was larger over the right hemisphere than over the left hemisphere. This is the typical N400 scalp distribution (Kutas & Hillyard, 1988). This pattern led to a significant main effect of left–right electrode position [$F(2,38) = 7.18$, $p < .05$], but the effect of anterior–posterior electrode position did not reach significance in the ANOVA ($p > .1$).

In the precue condition, a robust N400 component was present for valid trials, but very little N400 activity was present for invalid trials, consistent with the hypothesis that precues influence target identification. In the simultaneous cue condition, substantial N400 activity was observed on both valid and invalid trials, with approximately equal N400 amplitudes for valid and invalid trials in the initial portion of the N400 (ca. 300–500 msec). This pattern indicates that simultaneous cues do not influence target identification. The N400 effect in the simultaneous cue condition became slightly larger for validly cued targets than for invalidly cued targets after approximately 500 msec poststimulus (see Figure 5), which presumably reflects an influence of postperceptual processing on the continued semantic comparison between the target word and the context word.

The finding of a robust cue validity effect for precues but not for simultaneous cues led to a significant interaction between cue timing and cue validity [$F(1,19) = 9.22$, $p < .01$]. These factors did not significantly interact with the electrode factors.

Several planned follow-up analyses were conducted, paralleling the behavioral analyses. First, we conducted separate ANOVAs on the precue and simultaneous cue conditions. A significant cue validity effect was obtained in the precue condition [$F(1,19) = 18.99$, $p < .001$], but not in the simultaneous cue condition ($F < 1$). Second, we conducted separate analyses of the valid and invalid trials. For valid trials, the N400 was found to be significantly larger in the precue condition than in the simultaneous cue condition [$F(1,19) = 4.85$, $p < .05$]. For invalid trials, in contrast, the N400 was found to be significantly larger in the simultaneous cue condition than in the precue condition [$F(1,19) = 6.79$, $p < .02$]. These statistical comparisons confirm the observations that (a) cue validity influenced N400 amplitude only in the precue condition, and (b) precues led to enhanced N400 amplitude on valid trials and decreased N400 amplitude on invalid trials relative to the corresponding trials in the simultaneous cue condition.

Discussion

These results provide support for three interrelated hypotheses. First, cues can influence perceptual quality only when they precede the formation of a perceptual representation of the target; target perception is therefore not influenced by simultaneous cues under typical conditions. Consequently, cue validity did not influence N400 amplitude in the simultaneous cue condition. Second, when a cue and target appear simultaneously, the perceptual processing of the target suffers from some interference due to the simultaneous processing of the distractors. Consequently, both accuracy and N400 amplitude were reduced on valid trials in the simultaneous cue condition compared to the precue condition. Third, cues can influence postperceptual processes even when they do not precede the target information. Consequently, the simultaneous cues strongly influenced behavioral performance even though they did not influence the N400 component.

These conclusions require a few caveats, however. First, it is important to consider whether the N400 component is a sensitive measure of perceptual quality. It is possible, for example, that small changes in perceptual quality lead to large changes in N400 amplitude or, conversely, that a large N400 component can be observed even for low levels of perceptual quality. We have addressed the relationship between N400 amplitude and perceptual quality in a previous experiment by adding simultaneous masking noise to the target stimulus (Vogel, Luck, et al., 1998, Experiment 3). We varied the contrast of the masking noise over a broad range to manipulate the perceptual quality of the target, and we found that progressive increases in noise contrast caused progressive decreases in N400 amplitude, as measured from unrelated-minus-related difference waves. Thus, the N400 component provides a sensitive measure of variations in perceptual quality.

However, there is a second caveat regarding the use of the N400 component to assess perception. Specifically, although N400 amplitude varies according to perceptual quality, it may also be influenced by postperceptual factors. In particular, it is plausible that a word could be identified but not compared to the previously established semantic context, which would lead to no N400 in the unrelated-minus-related difference waves. Thus, the reduction in N400 observed on invalid trials compared to valid trials in the precue condition could reflect an impairment in postperceptual processing rather than an impairment in perceptual processing. Consequently, we cannot conclude with absolute certainty that perceptual processing was impaired on invalid trials in the precue condition. However, we can conclude with certainty that perceptual processing was unaffected by cues in the simultaneous cue condition. We can also conclude that the initial locus of selection was earlier in the precue condition (leading to a suppression of the N400 on invalid trials) than in the simultaneous cue condition (leading to no suppression of the N400 on invalid trials). Moreover, previous ERP and single-unit studies have demonstrated that precues lead to modulations of sensory processing (see reviews by Hillyard et al., 1998; Mangun, 1995). Thus, it is very likely that perception was impaired on invalid trials relative to valid trials in the precue condition.

Two broad conclusions can be drawn from these findings. First, the results of this experiment demonstrate that the locus of selection can be manipulated within a single experimental paradigm by manipulating the cue–target SOA. Thus, the results converge with the results obtained by Lavie (1995, 1997). Moreover, the present results cannot be explained by a difference in the effectiveness of selection at a single stage.

The second implication of these results is that it validates the logic shown in Figure 1. That is, any cueing effects obtained with simultaneous cues or postcues must reflect postperceptual mechanisms of attention (except under unusual conditions), and the finding of cueing effects with precues but not with simultaneous cues or postcues suggests a perceptual locus of attention (although this conclusion is somewhat weaker, as discussed below). Thus, by varying the cue–target SOA in a cueing experiment, it is possible to provide evidence about whether the cueing effects reflect an early-selection mechanism (leading to cueing effects only with precues), a late-selection mechanism (leading to equal cueing effects with precues and simultaneous cues), or a combination of both (leading to larger effects for precues than for simultaneous cues but substantial effects for both). The following experiments demonstrate the use of this logic to assess the locus of selection in behavioral paradigms.

EXPERIMENTS 2 AND 3

The goal of Experiments 2 and 3 was to provide a new form of behavioral evidence that the locus of selection can vary within a single experimental paradigm. Like the studies of Lavie and her colleagues, manipulations of load were used to induce changes in the locus of selection. However, we used a cueing task rather than a flankers task, and we varied both perceptual load and working memory load. To accomplish this, we compared a ‘‘memory-intensive task,’’ which was designed to isolate the operation of attention within visual working memory (Experiment 2), with a ‘‘perception-intensive task,’’ which was designed to isolate the operation of attention within visual perception (Experiment 3).

The Memory-Intensive Task (Experiment 2)

As illustrated in Figure 6A, the memory-intensive task combined a spatial cueing procedure with the visual working memory task that was developed by Luck and Vogel (1997) (see also Vogel, Woodman, & Luck, 2001). In the working memory task, observers were presented with a ‘‘sample array’’ consisting of 10 colored squares, 5 in each hemifield. After a brief delay, memory was tested for the colors in one hemifield by means of a ‘‘test array’’ that was presented in either the left visual field (LVF) or the right visual field (RVF). This array was identical to the portion of the sample array that had been presented in the same visual field, except that one of the squares changed to a new color on 50% of trials. The observers were asked to make an unspeeded response to indicate whether the colors in the test array matched the colors in the corresponding portion of the sample array.

A central arrow cue was also presented on each trial, indicating which side was likely to be tested. Specifically, when the cue pointed to a given visual field, the test array appeared in that visual field with 82% probability and appeared in the opposite visual field with 18% probability. A double-headed arrow was presented on 15% of trials, and on those trials the test array appeared with equal probability in the LVF and RVF.

Visual working memory has a capacity of only 3–4 objects in this task (Vogel, Woodman, & Luck, 2001;

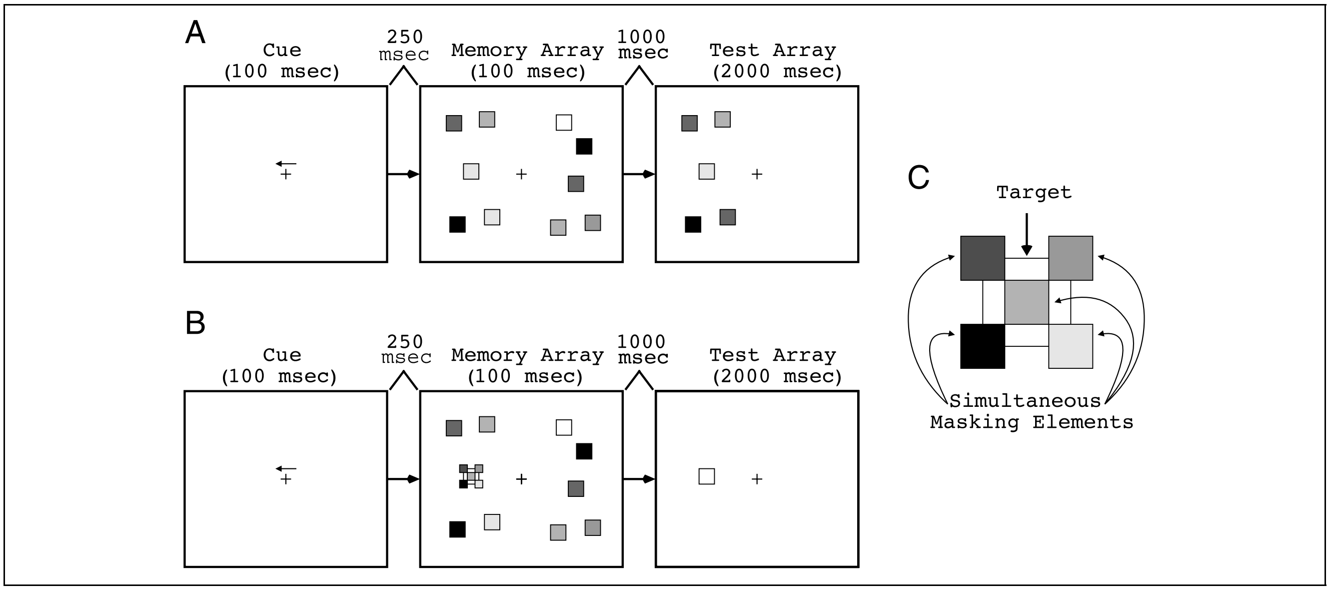

Figure 6. Example stimuli from the precue conditions of the memory-intensive task (A) and the perception-intensive task (B), with a close-up view of the target and simultaneous masking noise used in the perception-intensive task (C). In the memory-intensive task, the cue was used to indicate which set of five colors from the memory array was most likely to be tested in the test array. In the perception-intensive task, the cue was used to indicate which side of the memory array was most likely to contain the target item, which was always tested in the test array. In both tasks, the cue could appear 350 msec before the onset of the memory array, simultaneously with the memory array, or 350 msec after the onset of the memory array.

Luck & Vogel, 1997), and the 10 objects in the sample array therefore greatly overloaded the visual working memory system. Consequently, the observers should have been highly motivated to store only the cued objects in working memory. However, the visual system can easily identify a set of 10 highly discriminable colors (as demonstrated for these stimuli by Vogel, Woodman, & Luck, 2001, in press), so this task does not overload perception, and the cues should not influence the perceptual analysis of the sample array. That is, attention should operate at a late stage to influence the transfer of perceptual representations into working memory, but attention should not operate at an early stage to influence the formation of the perceptual representations.

To verify that attention operated postperceptually in this paradigm, we used the logic developed in Experiment 1 and tested precues, simultaneous cues, and postcues. The precues preceded the onset of the sample array by 350 msec, and the postcues followed the onset of the sample array by 350 msec.

We predicted that change-detection performance would be most accurate on valid trials, least accurate on invalid trials, and intermediate on neutral trials. We further predicted that the validity effect would be identical for precues and simultaneous cues, indicating that attention operates solely at a postperceptual stage in this paradigm. Some decrement in the cueing effect was possible in the postcue condition, because the delay between the offset of the sample array and the onset of the cue was long enough that some decay of the perceptual representation of the sample array was likely to occur before the onset of the cue. However, we expected to observe at least some effect of cue validity in this condition.

The Perception-Intensive Task (Experiment 3)

As illustrated in Figure 6B, the perception-intensive task was nearly identical to the memory-intensive task, but it increased the perceptual load and minimized the working memory load. To accomplish this, one item in the sample array served as the target, and it was obscured by simultaneous masking noise consisting of five small colored squares that occluded most of the target item. The masked target was the only item that the observers were required to remember, because the test array consisted of a single item at the location that had been occupied by the target. In this task, the cue predicted which side of the sample array would contain the target rather than indicating which side would be tested. Thus, the observers should have been motivated to enhance perceptual processing on the cued side, because a difficult-to-perceive object (the masked target) was likely to appear on this side. However, because they needed to store only this one object in working memory, the observers should have been motivated to remember whatever information was perceived about the target whether it appeared on the cued side or on the uncued side. Thus, we expected cue-directed attention to influence the formation of a perceptual representation of the target but not the transfer of this representation into working memory.

Because pilot testing indicated that postcues did not influence performance in the perception-intensive task, only precues and simultaneous cues were tested in this experiment. We predicted that the cues would be effective only in the precue condition because a simultaneous cue would be too late to influence the formation of a perceptual representation of the cued item.

Results

The results are summarized in Figure 7. Accuracy is summarized as percentage correct, averaging across change and no-change trials (the same pattern of results was obtained when accuracy was quantified with the d' measure of detection sensitivity). Separate ANOVAs were performed for each experiment with factors of cue validity (valid, neutral, invalid) and cue timing (precue, simultaneous cue, postcue for Experiment 2; precue, simultaneous cue for Experiment 3).

For both the memory-intensive task and the perception-intensive task, accuracy in the precue condition was high on valid-cue trials, substantially lower on neutral-cue trials, and quite low on invalid-cue trials. This led to a significant main effect of cue validity in both Experiment 2 [$F(2,18) = 137.08, p < .001$] and Experiment 3 [$F(2,18) = 12.01, p < .001$]. In the memory-intensive task, the cueing effect was almost exactly the same for the precue and simultaneous cue conditions and was only slightly smaller in the postcue condition. Consequently, there was no significant main effect of cue timing ($F < 1$) and no significant interaction between cue validity and cue timing ($p > .15$) for Experiment 2. In the perception-intensive task, however, cue validity influenced performance only with precues, leading to a significant interaction between cue validity and cue timing [$F(2,18) = 17.18, p < .001$].

Separate one-way ANOVAs were also conducted for each cue timing condition in each experiment. In the memory-intensive task (Experiment 2), a highly significant effect of cue validity was found for precues, simultaneous cues, and postcues (all ps $< .001$). In the perception-intensive task (Experiment 3), a significant cue validity effect was found for precues ($p < .001$) but not for simultaneous cues ($F < 1$).

To demonstrate that the effects of cue validity depended on the timing of the cue for the perception-intensive task but not for the memory-intensive task, we entered the data from both experiments into a single ANOVA with factors of task (memory-intensive, perception-intensive), cue validity (valid, neutral, invalid), and cue timing (precue, simultaneous cue; the postcue condition of Experiment 2 was excluded from this analysis because there was no postcue condition in Experiment 3). This ANOVA yielded a significant interaction between these three factors [$F(2,36) = 10.18, p < .001$], supporting the conclusion that cueing effects were present for both precues and postcues in the memory-intensive task but were present only for precues in the perception-intensive task.

Discussion

The memory-intensive condition produced large and significant cue validity effects in each of the cue timing conditions. Although we cannot conclude that the validity effects were identical across these conditions (which would require accepting the null hypothesis), we can conclude that cues were highly effective even

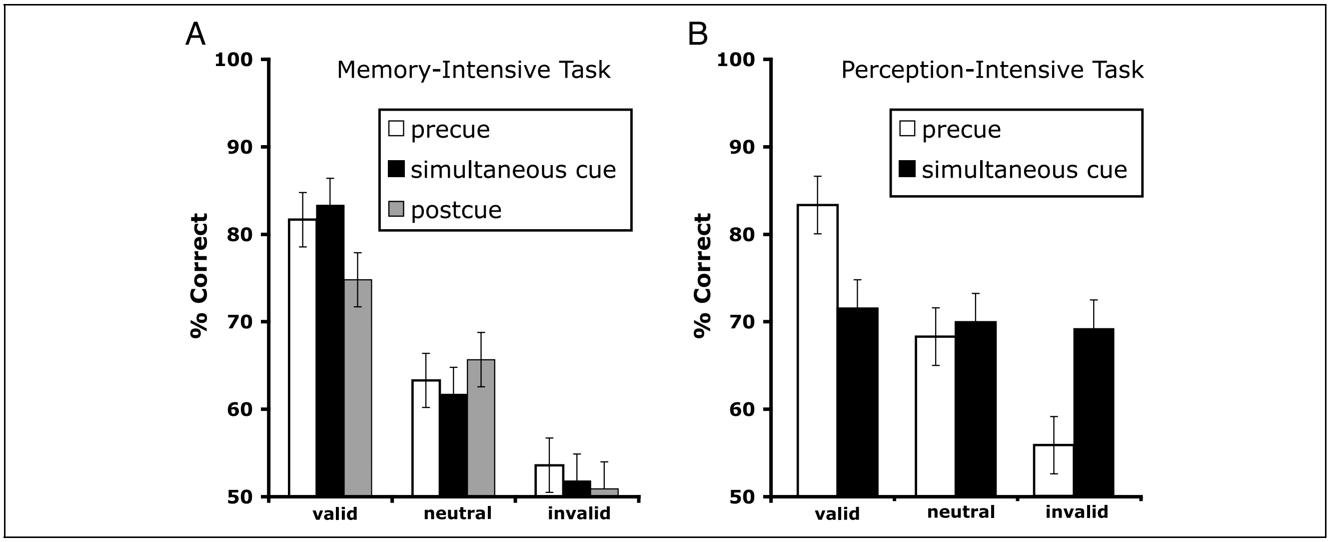

Figure 7. Mean accuracy as a function of cue–target delay for valid, neutral, and invalid trials for (A) the memory-intensive task used in Experiment 2 and (B) the perception-intensive task used in Experiment 3.

when they were presented 250 msec after the offset of the sample array in this task. Moreover, the cue validity effect was numerically almost identical for the precue and simultaneous cue conditions in the memory-intensive task. This pattern of results is consistent with an entirely postperceptual locus of selection. Thus, when the perceptual load is low and the working memory load is high, attention clearly operates at a late stage, and probably only at a late stage.

The perception-intensive task led to a large and significant cue validity effect in the precue condition but not in the simultaneous cue condition. This is exactly what would be expected if the cue influenced the formation of a perceptual representation of the to-be-remembered item but did not influence the transformation of perceptual representations into working memory representations. That is, a precue led to an enhanced perceptual representation of the masked item when it appeared on the cued side compared to the uncued side, but whatever perceptual information was available was transferred into working memory equally well whether the masked item appeared on the cued side or on the uncued side.

The pattern of results obtained for the perception-intensive task is similar to many previous reports of the effectiveness of a spatial cue across different cue-to-target SOAs. Under circumstances in which a single, difficult-to-discriminate target must be identified, a simultaneous cue is essentially as ineffective as having no cue at all. This pattern is quite different from the pattern observed for the memory-intensive task, in which cues were effective in the memory-intensive task even when they appeared 250 msec after the offset of the target information. These different patterns indicate that the perception-intensive and memory-intensive tasks do indeed isolate the operation of attention within different cognitive subsystems.

Before accepting this conclusion, however, it is important to consider an alternative explanation for the lack of a cue validity effect with simultaneous cues in the perception-intensive task. Specifically, it might be argued that the cue does not really provide any information in this condition, because the simultaneous masking noise unambiguously indicates the position of the target. That is, observers would have no motivation to attend to the side indicated by a probabilistic central cue given that the masking noise is a perfect indicator of the target's location. If this were true, then subjects could have also ignored the central cue and used the masking noise for this purpose in the precue condition as well as the postcue condition; the finding of a large validity effect only in the precue condition therefore provides evidence against this alternative explanation. However, the fact that the precue, but not the simultaneous cue, provided information about the likely target location prior to the masking noise makes it possible that subjects used the precue but not the postcue. We therefore conducted an additional experiment to demonstrate that the same pattern of results can be observed when this potential problem is eliminated.

EXPERIMENT 4

This experiment was largely identical to the perception-intensive task that was used in Experiment 3 except that two masked items were present on each trial, one in each hemifield. The cue indicated which of these two masked items was most likely to be tested. Although this increases the working memory demands of the task, two items are still well within the typical memory capacity. Thus, we predicted that cue validity would influence performance in the precue condition but not in the simultaneous cue condition.

Results and Discussion

The results of Experiment 4 are summarized in Figure 8. As in Experiment 3, a large cue validity effect was observed in the precue condition but not in the simultaneous cue condition. This led to a significant interaction between cue timing and cue validity [$F(1,9) = 7.41$, $p < .02$]. The main effects of cue timing and cue validity did not approach significance ($p > .6$ and $p > .15$, respectively). Separate analyses of the precue and simultaneous cue conditions yielded a significant cue validity effect for precues [$F(2,18) = 4.47, p < .05$] but not for simultaneous cues ($F < 1$).

These results indicate that the finding of significant cue validity effects only when the cue preceded

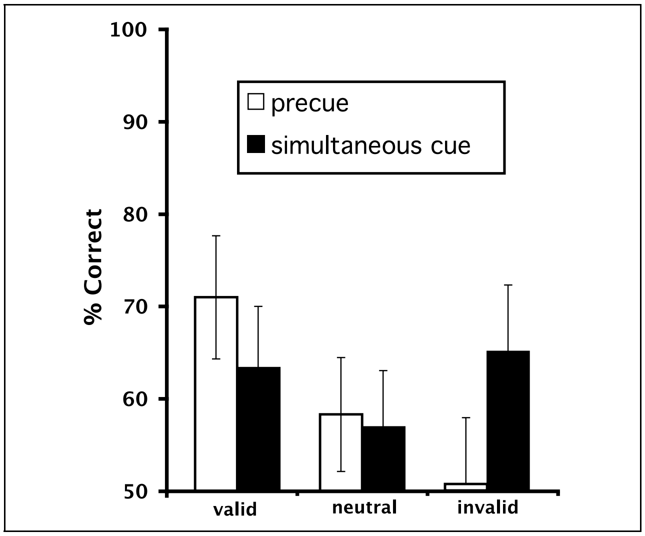

Figure 8. Mean accuracy as a function of cue–target delay for valid, neutral, and invalid trials for the perception-intensive task used in Experiment 4.

the sample array in Experiment 3 cannot be explained by postulating that the cue provided no unique information in the simultaneous cue condition. That is, subjects in the perception-intensive task used in Experiment 3 may have ignored the cue because the simultaneous masking noise provided more reliable information about the location of the target, but this cannot explain the results of the present experiment. Instead, the observed pattern of results provides evidence that attention primarily influences the formation of perceptual representations in this perception-intensive task.

GENERAL DISCUSSION

Previous studies have shown that attention operates in different neural and cognitive systems under different conditions, which is consistent with the flexible-selection hypothesis. However, the complex theoretical construct of attention has been operationalized in very different ways in these different experiments, and it is not clear that the same construct is being assessed in paradigms as diverse as visual search, spatial cueing, the Stroop and flankers tasks, the attentional blink task, and the continuous performance task. The present study focused on a well-defined variety of selective attention, as operationalized by cue validity effects in a spatial cueing paradigm, and demonstrated that the locus of attention can shift between perceptual and postperceptual systems with modest manipulations to a given task.

Experiment 1 demonstrated that attention can operate at both perceptual and postperceptual stages when the cue precedes the target information but operates only postperceptually when the cue appears simultaneously with the target. When precues were used, the N400 data indicated that target identification was impaired at uncued locations, which is consistent with previous ERP studies showing reduced sensory responsiveness at uncued locations (see reviews by Hillyard et al., 1998; Mangun, 1995). When simultaneous cues were used, the N400 data indicated that the target was perceived equally well at the cued and uncued locations, even though behavioral accuracy was impaired at the uncued locations. This is exactly what would be expected if attention operated solely at a postperceptual stage with simultaneous cues.

Experiments 2–4 extended these results, showing that attention can operate solely at a perceptual stage or solely at a postperceptual stage depending on whether perceptual or postperceptual systems were overloaded. These results converge with experiments using the flankers paradigm to show that early selection occurs only when perception is overloaded (e.g., Lavie & Cox, 1997; Lavie, 1995), and they go further by demonstrating that the operation of attention in working memory depends on whether working memory is overloaded.

Now that it is clear that the locus of selection can vary flexibly within a single task, it is important to consider whether attention is a unified, monolithic system or a set of computationally similar but independent processes that operate within different neural and cognitive subsystems under different conditions. There is evidence for both of these possibilities. For example, neuroimaging evidence implicates a region of the intraparietal sulcus in a large variety of attention-demanding tasks (Shafritz, Gore, & Marois, 2002; Marois, Chun, & Gore, 2000; Wojciulik & Kanwisher, 1999). That is, whenever conditions of competition exist that demand the focusing of attention, this region of the intraparietal cortex appears to be engaged. Thus, a centralized system may play a key role in all varieties of visual attention.

On the other hand, it seems likely that attention must operate according to somewhat different principles in different neural and cognitive systems, reflecting differences in the computations and representational formats used in these different systems. Evidence for this comes from studies of the ability of attention to be focused simultaneously on noncontiguous areas of space. One might expect that the spatiotopic organization of early and intermediate visual areas would lead to attractor dynamics that would make it difficult to maintain two separate attended regions. In contrast, higher-level representations of objects are not organized in a detailed spatiotopic fashion, so it may be possible to distribute attention in a more flexible manner in these higher-level representations. When Heinze, Luck, et al. (1994) isolated early selection by examining the P1 wave in ERP recordings, attention was found to be focused on a single contiguous region, with no evidence for multiple discontinuous foci of attention. In contrast, memory-intensive behavioral paradigms have found clear evidence that attention can be divided into discontinuous regions (e.g., Awh & Pashler, 2000). Vogel (2000) examined this issue using the memory-intensive and perception-intensive cueing paradigms described in Experiments 2 and 3, and he found that attention could be split into discontinuous foci in the memory-intensive task but not in the perception-intensive task. Thus, the spatial properties of attention may reflect the spatial properties of the system in which attention is currently operating.

In addition to this evidence for different operating characteristics of attention within different neural and cognitive systems, there is also some evidence that attention can be simultaneously focused on different sources of information in different systems. Specifically, Woodman, Vogel, and Luck (2001) found that subjects could efficiently shift perceptual attention mechanisms from object to object in a visual search task while visual working memory was filled to capacity with a different set of objects. Some researchers posit that maintaining objects in working memory requires focusing attention onto those objects (e.g., Cowan, 1997), and the results of Woodman et al. therefore suggest that attention can be focused on one set of items in perception, whereas attention is focused on another set of items in working memory.

Thus, there is some evidence for a unitary attentional system that operates within multiple neural and cognitive systems, and there is some evidence that attention operates somewhat autonomously within different systems. It is possible that some neural systems are engaged whenever attention is needed but others are engaged more selectively and independently. Further research will be necessary to address this possibility, and the methods and findings of the present study should be useful in understanding how attention works in a variety of cognitive and neural systems.

METHODS

Experiment 1

Subjects

Twenty students between the ages of 18 and 30 were paid to participate in this experiment. They reported having normal color vision, normal or corrected-to-normal visual acuity, and no history of neurological problems.

Stimuli and Procedure

Chromaticity (*x* and *y*) and luminance values for the stimuli were measured with a Tektronix model J17 colorimeter and are reported here using the 1931 Commission International d'Eclairage color coordinate system. The stimuli were presented on a video display in white (13.04 cd/m^2) on a black background at a distance of 70 cm. As illustrated in Figure 2, each trial in the precue condition began with the presentation of a fixation point in the center of the display. After 2000 msec, a context word was presented in the center of the screen for 1000 msec. This was followed by a 1000-msec presentation of the fixation point and then a 1000-msec presentation of a cue, which was a 0.7° arrow that was centered at the point of fixation and pointed up, down, left, or right. The cue was followed by a 1000-msec presentation of the fixation point and then a 100-msec presentation of a target array, a 67-msec blank period, and then a 500-msec presentation of a mask array (the fixation point was visible during all of these periods).

The target and mask arrays each contained four character strings, centered 2.9° above, below, to the left of, and to the right of the fixation point. In the target array, one of these character strings was a target word and the other three were strings of randomly selected consonants. The target word appeared at the cued location on 75% of trials and at a randomly selected uncued location on 25% of trials. All four character strings in the mask array were strings of randomly selected consonants (new random selections rather than repetitions of the strings in the target array). After the mask was presented, the fixation point remained visible for an additional 1000 msec and was then replaced by a question mark for 2000 msec. The question mark indicated that it was time for the subject to respond.

The simultaneous cue condition was identical to the precue condition, except that the precue interval was replaced by a fixation interval, and the cue was presented simultaneously with the target array.

Each word or consonant string in this experiment contained between four and seven characters and measured 0.7° vertically and 1.9–5.0° horizontally. The words were selected from a list of 360 pairs of highly related words (see Vogel, Luck, et al., 1998 for details). The target word was semantically related to the context word on 50% of trials; on these trials, the context word and the target word were the two members of a pair in this list. On the remaining 50% of trials, the context word and the target word were selected from different pairs in the list and were usually semantically unrelated (although this was not guaranteed on all trials given that the two words were selected randomly). Related and unrelated words occurred with equal probability on valid and invalid trials.

Subjects were instructed to make an unspeeded button-press response on a game pad at the end of each trial, pressing with the index finger of one hand if the target word was semantically related to the context word and pressing with the index finger of the other hand if the target word was unrelated. The mapping was counterbalanced across subjects. Subjects were informed about all of the probabilities.

The precue and simultaneous cue conditions were randomly intermixed within trial blocks, and subjects could not anticipate which type of trial would occur next. Each block contained 48 trials in random order, and 10 blocks were tested. Subjects experienced approximately 20 practice trials before the experiment began.

Recording and Analysis

The electroencephalogram (EEG) was recorded from tin electrodes in an elastic cap (Electrocap International; Eaton, OH), using a subset of the International 10/20 System sites (F3, F4, C3, C4, P3, P4, T3, T4, T5, T6, O1, and O2). These sites, along with a left-mastoid site, were recorded using a right-mastoid reference electrode, and the signals were re-referenced off-line to the average of the left and right mastoids. The horizontal electrooculogram (EOG) was recorded as the voltage between electrodes placed 1 cm lateral to the external canthi and was used to measure horizontal eye movements. The vertical EOG was recorded from an electrode beneath the left eye, referenced to the right mastoid, and was used to detect blinks and vertical eye movements. The EEG and EOG were amplified by an SA Instrumentation amplifier with a gain of 20,000 and a bandpass of 0.01–80 Hz, and the amplified signals were digitized at 250 Hz by a PC-compatible computer and averaged off-line. Trials with ocular artifacts were excluded from the averages, but trials with incorrect behavioral responses were not excluded because we expected to observe dissociations between the electrophysiological responses and behavioral accuracy. Trials with ocular artifacts (blinks and eye movements) were excluded from all analyses (this was 13.3% of trials).

To isolate the N400 component, we constructed difference waves in which the ERP waveforms from semantically related trials were subtracted from the ERP waveforms from semantically unrelated trials. We then quantified N400 amplitude in these difference waves by measuring the mean amplitude between 300 and 700 msec poststimulus, relative to a 200-msec prestimulus baseline. Measurements were obtained at the frontal, central, and parietal electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4). Within-subjects ANOVAs were used for all statistical analyses, and the p values were adjusted in accordance with the Greenhouse–Geisser epsilon value.

Experiment 2

Subjects

Ten students between the ages of 18 and 30 participated in this experiment for course credit or monetary compensation. They reported having normal color vision, normal or corrected-to-normal visual acuity, and no history of neurological problems.

Stimuli

The stimuli were presented on a video display at a distance of 70 cm. The background was gray (8.2 cd/m^2), and a fixation cross was continuously visible in the center of the display. Each sample array consisted of 10 colored squares, 5 in the LVF and 5 in the RVF. They were presented within two $4^\circ \times 7.3^\circ$ regions that were centered 3° to the left and right of fixation. Stimulus positions were randomized on each trial, with the constraint that the distance between squares was at least 2° (center to center). Each square subtended $0.65^\circ \times 0.65^\circ$ of visual angle. The color of each square was randomly selected from a set of seven colors: white (92.46 cd/m^2), red ($x = 0.642, y = 0.327$; 22.62 cd/m^2), blue ($x = 0.152, y = 0.067$; 9.66 cd/m^2), green ($x = 0.318, y = 0.569$; 64.99 cd/m^2), black (<0.01 cd/m^2), yellow ($x = 0.478, y = 0.452$; 65.23 cd/m^2), and violet ($x = 0.304, y = 0.149$; 7.04 cd/m^2). A given color could appear no more than twice within an array.

Each test array was identical to the left or right half of the preceding sample array, except that one of the squares changed to a different, randomly selected color on 50% of trials. The cue was a white, horizontally oriented, single-headed or double-headed arrow. It subtended 1.25° of visual angle and was presented 0.65° above the fixation point.

Procedure

Each trial began with a 100-msec period that contained a cue in the precue condition and nothing (except the continuously visible fixation point) in the simultaneous cue and postcue conditions. This was followed by a 250-msec blank period and then a 100-msec presentation of the sample array. In the simultaneous cue condition, the cue was present during the presentation of the sample array. The sample array was followed by a 250-msec blank period and then a 100-msec period during which the cue was presented in the postcue condition or a 100-msec blank period in the precue and simultaneous cue conditions. This was followed by another 650-msec blank interval and then a 2000-msec presentation of the test array. Each trial was followed by a 1000-msec intertrial interval.

Subjects were instructed to remember the colors in the sample array and determine whether the items in the test array were identical to the corresponding items in the sample array or whether one item changed in color. They pressed one button on a game pad when a change was detected and a different button when no change was detected. Accuracy was stressed rather than speed. Change and no-change trials were equiprobable and occurred in random order. The subjects were informed about the cue probabilities.

To rule out potential contributions from verbal working memory, subjects performed a concurrent articulatory suppression task during each trial. Specifically, before each trial, they were presented with two numerals, and they were required to repeat these two numerals aloud throughout the course of each trial (e.g., ‘‘four–seven, four–seven, four–seven,’’ etc.). If the subject failed to repeat the numerals during the entire course of the trial, that trial was excluded from any further analyses. However, this was exceptionally rare (less than 1% of trials). This articulatory suppression task has previously been demonstrated to be highly effective at deterring the use of a verbal encoding strategy in this type of task (Vogel, Woodman, & Luck, 2001). The numerals were presented for 1000 msec at the beginning of the trial, followed by a 1000-msec blank interval.

The precue, simultaneous cue, and postcue conditions were randomly intermixed within trial blocks, as were valid, invalid, and neutral trials. For each SOA condition, each subject performed an average of 98 valid trials, 21 neutral trials, and 21 invalid trials that were randomly mixed within a single block of trials.

Eye Movement Recordings

To ensure that the cueing effects reflected covert shifts of attention rather than overt eye movements, subjects in all experiments reported here were instructed to maintain fixation at all times, and eye movements were assessed by means of EOG recordings using the methods of Experiment 1. Trials with clear eye movements (typically 1° or larger) were excluded from all data analyses.

Experiment 3

The method was identical to that of Experiment 2 except as follows. A new set of 10 subjects was tested. One item in the sample array was obscured by a set of five small colored squares ($0.12^\circ \times 0.12^\circ$) that were centered over the corners and center of one target square. The colors of these small squares were selected, without replacement, from the same set of colors used in the sample array. The subjects' task was to remember the color of the masked item. The test array consisted of a single item presented at the location that had been occupied by the masked item, and the test item was either the same color as the masked item or a new color (the one color that was neither the target color nor the color of any of the masking elements).

The cues were identical to those in Experiment 1, except that only the precue and simultaneous cue conditions were tested. When one side was cued, the masked item appeared on that side with a probability of .82 and on the opposite side with a probability of .18. On neutral trials, the masked item appeared equally often on the two sides. The test item always appeared at the location of the masked item. Thus, whereas the cue predicted the side of the test array in Experiment 1, it predicted the side of the masked item within the sample array in the present experiment.

Experiment 4

Ten new subjects participated in this experiment. The method was identical to that of Experiment 3 except that two masked items were presented in each sample array, one in each visual field, along with four unmasked items in each visual field. The cue predicted which of these masked items was likely to be tested rather than indicating the side on which the masked item would likely occur. This made the design even closer to that of Experiment 2, in which the cue also predicted which side was likely to be tested.

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Notes

1. We use the term perception to refer to the formation of high-level representations of sensory inputs, whether or not those representations are available to awareness.
2. If the cue leads to a very rapid shift of attention and perceptual processing is extended over a long period (as in a visual search task), it is possible that a cue presented simultaneously with or after a target could influence perceptual processing of the target. However, the logic developed here should apply to the majority of cueing paradigms.
3. It should be noted that attention might also operate in this paradigm by giving the cued location more weight in the decision process (Luck, Hillyard, Mouloua, & Hawkins, 1996; Shiu & Pashler, 1994), but this is also presumed to be a post-perceptual process.

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