

Orienting Attention to Locations in Internal Representations

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Abstract

■ Three experiments investigated whether it is possible to orient selective spatial attention to internal representations held in working memory in a similar fashion to orienting to perceptual stimuli. In the first experiment, subjects were either cued to orient to a spatial location before a stimulus array was presented (pre-cue), cued to orient to a spatial location in working memory after the array was presented (retro-cue), or given no cueing information (neutral cue). The stimulus array consisted of four differently colored crosses, one in each quadrant. At the end of a trial, a colored cross (probe) was presented centrally, and subjects responded according to whether it had occurred in the array. There were equivalent patterns of behavioral costs and benefits of cueing for both pre-cues and retro-cues. A follow-up experiment used a peripheral probe stimulus requiring a decision about whether its color matched that of the item presented at the

same location in the array. Replication of the behavioral costs and benefits of pre-cues and retro-cues in this experiment ruled out changes in response criteria as the only explanation for the effects. The third experiment used event-related potentials (ERPs) to compare the neural processes involved in orienting attention to a spatial location in an external versus an internal spatial representation. In this task, subjects responded according to whether a central probe stimulus occurred at the cued location in the array. There were both similarities and differences between ERPs to spatial cues toward a perception versus an internal spatial representation. Lateralized early posterior and later frontal negativities were observed for both pre- and retro-cues. Retro-cues also showed additional neural processes to be involved in orienting to an internal representation, including early effects over frontal electrodes. ■

INTRODUCTION

To interact successfully in the spatial world we need both to be able to attend selectively to items in the extra-personal world and to those maintained in mind as mental representations. Although spatial orienting toward perceptual events has been intensively investigated, spatial orienting to internal representations has remained relatively unexplored. Here we investigated the behavioral and neural processes involved in orienting spatial attention selectively to information held in internal spatial representations in working memory (WM), and compared them directly to orienting spatial attention to perceptual information.

The relationship between attentional operations in perception and WM has been highlighted by several lines of research. Graziano, Hu, and Gross (1997) demonstrated that internal representations can be used to guide action toward previously seen perceptual stimuli that are no longer present. Internal spatial representations can also be impaired in certain cases of neglect (Bisiach & Luzzatti, 1978), sometimes selectively (Ortigue et al., 2001; Beschin, Cocchini, Della Sala, & Logie, 1997; Co-

slett, 1997; Guariglia, Padovani, Pantano, & Pizzamiglio, 1993). Other studies have demonstrated a link between actual perceptual events and internal “images,” both in terms of the influence of “holding images in mind” on behavioral performance (Downing, 2000; Pashler & Shiu, 1999; Farah, 1985; Ishai & Sagi, 1995), and similar regions of neural activation (Kosslyn, Ganis, & Thompson, 2001; Ishai, Ungerleider, & Haxby, 2000; O’Craven & Kanwisher, 2000). The Downing (2000) study showed that the contents of WM can guide selective attention. Unsurprisingly, influential theoretical models posit a close link between WM and the allocation of selective attention (e.g., Desimone & Duncan, 1995; Baddeley, 1993).

Convergent findings from different methodologies have shown that spatial attention and spatial WM are subserved by partially overlapping large-scale distributed systems of frontal and parietal areas (Pollmann & von Cramon, 2000; Awh et al., 1999; LaBar, Gitelman, Parrish, & Mesulam, 1999; McCarthy, 1995). This has led to the intuitively appealing suggestion that there may be similarities between the process of directing spatial attention to a location, and the process of holding a spatial location in WM (Awh & Jonides, 2001). Supporting evidence for this view comes from findings that stimuli appearing at memorized locations, and attended targets in spatial attention tasks exhibit a similar pattern of activation and

modulation in posterior extrastriate visual areas in both brain imaging (Awh et al., 1999) and event-related potential (ERP) (Awh, Anllo Vento, & Hillyard, 2000) studies.

Sperling (1960) developed an experimental paradigm that enables attention to be directed toward contents of mental representations. He used cues to orient participants to selective aspects of iconic traces of briefly presented visual arrays. The present experiments build on this by using cues to orient attention to locations of arrays held in WM, after the iconic trace period. Spatially informative cues were presented 1.5–2.5 sec before (pre-cue) or after (retro-cue) a stimulus array, which oriented subjects attention to either a perceptual location (pre-cue), or a specific location in the array that existed only as an internal representation in WM (retro-cue). We were firstly interested in whether it was possible to orient attention to selective locations of internal representations of previously presented stimuli held in WM; and, if so, whether it can provide similar behavioral advantages to those seen with spatially informative cues presented before the appearance of a stimulus array (Posner, 1980). Secondly, we wished to compare the neural process of orienting attention to internal mental representations to the better known literature relating to the orienting of visual attention to upcoming perceptual stimuli (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopf & Mangun, 2000; Hopfinger, Buonocore, & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Yamaguchi, Tsuchiya, & Kobayashi, 1994; Harter, Miller, Price, LaLonde, & Keyes, 1989), to see whether the same, different, or partially overlapping control systems are involved.

Many studies have used cues presented after a stimulus array to study cognitive processes. For example, Kinchla, Chen, and Evert (1995) cued peripheral locations to inform subjects which element in a briefly presented array was most likely to have been a predefined target stimulus. Other studies (Luck et al., 1994; Hawkins et al., 1990; Downing, 1988) have also used cues presented after a stimulus array, but to indicate which location in an array required a decision about the presence or the absence of a predefined target stimulus. Schmidt, Vogel, Woodman, and Luck (2002) also presented cues after a stimulus array, but in this case the cues were nonpredictive, peripheral transients, presented immediately after the array, to study the transfer of information into WM.

Recently, there have been studies examining ERPs to cues presented after arrays to be memorized, which instruct subjects what feature dimension is to be retrieved from stimuli held in WM (Bosch, Mecklinger, & Friederici, 2001; Mecklinger, 1998). However, these investigations have been primarily concerned with differences between retrieving spatial versus object information from WM, and the memory rehearsal processes involved in each case (Mecklinger, 1998; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1997).

The present experiments used cues presented after a stimulus array to orient attention selectively to locations in internal representations. The cues were presented within an interval where WM, and not iconic memory, operates. Unlike previous studies, the target stimuli were not defined before task performance, and the cues therefore did not guide response decisions. The cues were also centrally presented and informative.

In Experiment 1 (see Fig. 1A), subjects were given spatially informative cues (80% validity) to orient to a spatial location either before a stimulus array was presented (pre-cue), or after the array was presented (retro-cue), or given no cueing information (neutral cue). Subjects then decided whether a probe stimulus had been present in the array (50% probability). When the probe stimulus had been present in the array, the informative pre-cues and retro-cues predicted its correct location 80% of the time. Analysis of behavioral data revealed that it is possible and advantageous to orient attention selectively to locations in internal representations. Experiment 2 (see Fig. 1B) followed up from these findings to ensure that the behavioral effects did not reflect solely differences in response criteria between valid and invalid trials. The task and cueing conditions were equivalent to those in Experiment 1, except that a peripheral probe stimulus prompted a decision as to whether its color matched that of the item at the same location in the array (50% probability). This manipulation eliminated uncertainty about which location subjects should use in the decision process. In Experiment 3 (see Fig. 1C), ERPs were recorded while subjects performed a simplified version of the tasks with only pre-cue and retro-cue conditions. The probe stimuli were presented centrally, and subjects responded according to whether the probe stimulus occurred at the cued location (50% probability). Analysis of ERPs to the identical cueing stimuli occurring before versus after the array allowed us to compare the orienting of attention to a spatial location of an expected perceptual stimulus with orienting attention to an internal spatial representation of the same percept held in WM. Of specific interest was whether the same or different processes were involved in the two cases, and whether they had the same time course of operation.

EXPERIMENT 1: PREDICTING LOCATIONS IN EXTERNAL VERSUS INTERNAL SPACE

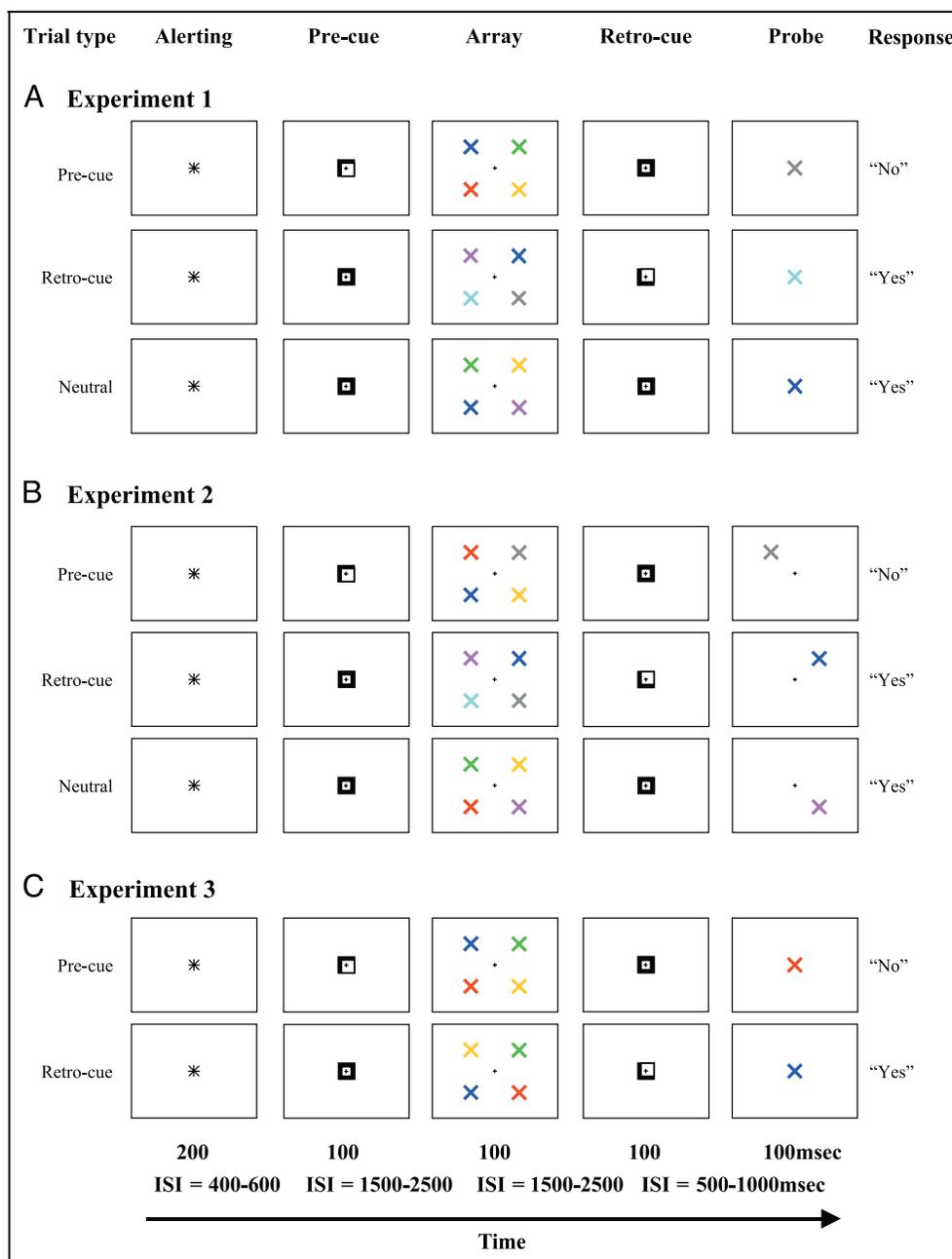
This experiment established that there were behavioral advantages of orienting to locations in both extrapersonal space and internal spatial representations.

Results

Reaction Times

The pattern of reaction time is shown in Figure 2A. The first comparison was between valid and invalid trials for

Figure 1. Schematics for experimental tasks. Stimulus durations and interstimulus intervals were the same in the three tasks. All trials contained a pre-cue (100 msec), an array of four differently colored crosses (100 msec), a retro-cue (100 msec), and a probe stimulus (100 msec). In pre-cue trials, the spatially informative orienting cue (80% validity) was presented before the stimulus array. In retro-cue trials, the spatially informative orienting cue (80% validity) was presented after the stimulus array. In neutral trials, there was no spatially informative orienting cue. (A) Experiment 1: In all trials subjects responded according to whether the central probe stimulus had been present in the array (50% probability). (B) Experiment 2: The probe stimulus was presented peripherally, at one of the four array locations, and subjects responded according to whether the probe stimulus matched the item presented at that location in the array (50% probability). (C) Experiment 3: There were only pre-cue and retro-cue trials. The central probe stimulus was always present in the array, and subjects responded according to whether it occurred at the cued location (50% probability).



pre-cues and retro-cues. There was a significant main effect of validity, $F(1,9) = 13.774$, $p = .005$, reflecting shorter reaction times in valid trials. There was no effect of cue type, or interaction between cue and validity. This indicates that the pattern of shortened reaction times for valid versus invalid trials was equivalent for pre-cues and retro-cues.

Reaction-time advantages for valid pre-cues and retro-cues relative to neutral cues were tested using a two-way repeated-measures analysis of variance (ANOVA) with factors of response (yes, no) and cue (pre, retro, neutral), using only valid pre-cue and retro-cue trials. There was a main effect of cue, $F(2,18) = 8.431$, $p = .012$, indicating differences in reaction times between the

three conditions. Post hoc contrasts revealed that neutral trials had longer reaction times than both pre-cue and retro-cue trials [pre-cue vs. neutral, $F(1,9) = 9.501$, $p = .013$; retro-cue vs. neutral, $F(1,9) = 8.666$, $p = .016$]. Reaction times in pre-cue trials versus retro-cue trials were equivalent. There was a main effect of response, $F(1,9) = 13.693$, $p = .005$, reflecting quicker responses to probes that had been present in the array ("yes" probes). There was also a significant interaction between the response and cue factors, $F(2,18) = 4.854$, $p = .032$. Post hoc contrasts revealed that the differences in reaction time between "yes" and "no" trials were larger for pre-cue and retro-cue trials compared to neutral trials (although the effect in retro-cue trials only tended

toward significance) [pre-cue/neutral \times yes/no, $F(1,9) = 7.031$, $p = .026$; retro-cue/neutral \times yes/no, $F(1,9) = 4.104$, $p = .073$]. There was no difference between pre-cue and retro-cue trials.

Reaction-time costs for invalid pre-cues and retro-cues relative to neutral cues were tested using a similar analysis with factors of response (yes, no) and cue (pre, retro, neutral), using only invalid pre- and retro-cue trials. There were no significant effects of cue, or interaction between cue and response. There was only a significant main effect of response, $F(1,9) = 6.680$, $p = .029$, again indicating shorter reaction times when the probe was present in the array.

Accuracy

The pattern of performance accuracy in the experimental conditions is shown in Figure 2B. The first comparison was between valid and invalid trials for pre-cues and retro-cues. There was a significant main effect of validity, $F(1,9) = 12.358$, $p = .007$, reflecting greater accuracy in valid trials. There was no effect of cue, or interaction between cue and validity. This indicates that the pattern of increased accuracy for valid versus invalid trials was equivalent for pre-cues and retro-cues.

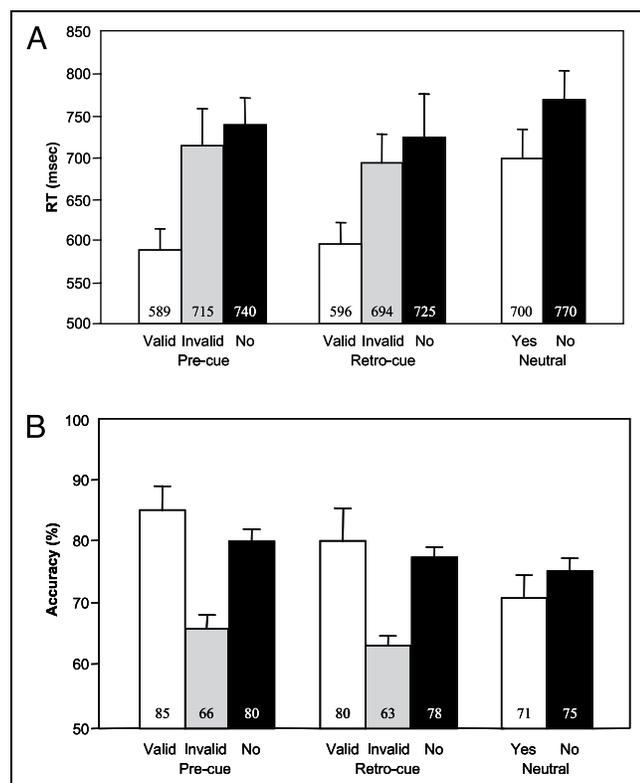


Figure 2. (A) Experiment 1: Mean reaction time (RT) and standard error for probe stimuli in pre-cue, retro-cue, and neutral trials, separated according to the factors of response and cue validity. (B) Experiment 1: Mean accuracy and standard error for probe stimuli in pre-cue, retro-cue, and neutral trials, separated according to the factors of response and cue validity.

Accuracy advantages for valid pre-cues and retro-cues relative to neutral cues were tested using a two-way repeated-measures ANOVA with factors of response (yes, no) and cue (pre, retro, neutral), using only valid pre-cue and retro-cue trials. There was a main effect of cue, $F(2,18) = 6.209$, $p = .023$, indicating differences in accuracy between the three cue types. Post hoc contrasts revealed that pre-cue trials had greater accuracy than neutral trials [pre-cue vs. neutral, $F(1,9) = 7.392$, $p = .024$]. Otherwise, accuracy did not differ between the conditions. There was no significant effect of response, indicating no differences in accuracy between “yes” and “no” trials. There was a significant interaction between response and cue, $F(2,18) = 4.663$, $p = .029$. Post hoc contrasts revealed that the interaction was due to the differences in accuracy between “yes” and “no” trials being greatest for pre-cue trials compared to neutral trials [pre-cue/neutral \times yes/no, $F(1,9) = 7.943$, $p = .020$].

Accuracy costs for invalid pre-cue and retro-cue trials relative to neutral cues were tested using a similar analysis with factors of response (yes, no) and cue (pre, retro, neutral), using only invalid pre- and retro-cue trials. There was no significant effect of cue, indicating no overall difference in accuracy between the three cue types. There was a significant main effect of response, $F(1,9) = 9.820$, $p = .012$, reflecting decreased accuracy in “yes” trials compared with “no” trials. There was a significant interaction between the response and cue factors, $F(2,18) = 4.191$, $p = .034$. Post hoc contrasts revealed that the difference in accuracy between “yes” and “no” trials (less accurate in “yes” trials) was greater in pre-cue and retro-cue trials than neutral trials [pre-cue/neutral \times yes/no, $F(1,9) = 5.722$, $p = .040$; retro-cue/neutral \times yes/no, $F(1,9) = 5.714$, $p = .041$]. There was no difference in the pattern of results between pre-cue and retro-cue trials.

Summary

The behavioral analyses showed that subjects have decreased reaction times and increased accuracy in valid trials compared to invalid trials. This pattern of results was the same for both pre-cues and retro-cues. Compared with neutral trials, subjects showed reaction-time advantages for valid trials, and accuracy disadvantages for invalid trials. These effects were equivalent for pre-cues and retro-cues. Pre-cues also showed accuracy advantages compared to neutral trials. Overall, reaction times were shorter for trials where the probe stimulus was present in the array compared with trials where it was not present in the array for all cue types (pre-cue, retro-cue, neutral).

Discussion

The aim of Experiment 1 was to investigate whether it is possible to orient selective spatial attention to internal representations in WM. We showed that it is possible to orient attention to internal spatial represen-

tations, at least when the number of items and features is within the limits of WM capacity (c.f. Wheeler & Treisman, 2002; Vogel, Woodman, & Luck, 2001; Luck & Vogel, 1997). Surprisingly, orienting to internal representations was characterized by an almost identical pattern of behavioral costs and benefits of cueing as orienting to spatial locations.

The results of Experiment 1 showed that there were similar behavioral benefits and costs of orienting attention to upcoming perceptual stimuli and to internal representations. In the pre-cue condition, the finding of faster reaction times to validly cued trials, and decreased accuracy to invalid trials, relative to neutral trials replicated the well-known effects of orienting spatial attention to visual arrays (e.g., Hawkins et al., 1990; Müller & Findlay, 1987; Müller & Rabbit, 1989; Jonides, 1981; Posner, 1980). The behavioral effects in the pre-cue condition are thus best conceptualized by both benefits of valid cueing, and costs of invalid cueing. Responses were also quicker in the pre-cue condition to probe stimuli that had appeared in the array than those that did not. Similar findings of faster responses to “yes” stimuli are common in the visual search literature (e.g., Chelazzi, 1999; Wolfe, 1994; Treisman & Gelade, 1980).

The findings of behavioral effects due to valid and invalid cueing in the retro-cue condition show that it is possible and advantageous to orient attention toward selective attributes of internal representations. Responses to valid cues were quicker, and responses to invalid cues were less accurate, than neutral trials. This was exactly the same pattern of behavioral costs and benefits seen in the pre-cue condition. Also, as in the pre-cue condition, responses were quickest for probe stimuli that had been presented in the array. A similar finding of faster responses to matching probe stimuli is typically found in delayed match-to-sample tasks (e.g., Klaver, Smid, & Heinze, 1999; Mecklinger, 1998).

This experiment was different to other studies using cues presented after a perceptual array in two main respects. Firstly, the response-relevant targets were not predetermined, but were only defined at the end of each trial by a separate probe stimulus. Secondly, retro-cues provided information about the likely location of the relevant target, but did not drive a response decision. In most previous experiments, targets were predefined (Kinchla et al., 1995; Luck et al., 1994; Hawkins et al., 1990; Downing, 1988). Post-cues signaled the location at which a decision was required (Luck et al., 1994; Hawkins et al., 1990; Downing, 1988), or provided information about target location (Kinchla et al., 1995). In the above experiments, the post-cues could facilitate decision making about whether a target was present or absent. The present task design separates orienting attention to mental representations from response decisions, and therefore the behavioral facilitation observed by retro-cues cannot be attributed merely to faci-

litating the decision about where a target stimulus might have been.

In a recent study, Schmidt et al. (2002, Experiment 4) presented nonpredictive peripheral cues immediately after stimulus array offset, and found memory for subsequent probe stimuli presented at the cued location to be better than memory for stimuli at uncued locations. Their results suggest that cues appearing after the offset of a visual stimulus can influence the transfer of perceptual information into visual WM. However, Schmidt and colleagues used nonpredictive, peripheral transients as cues, presented in the iconic memory period. The present study presented orienting cues after the iconic trace period, and demonstrated behavioral advantages of predictive, central cues that oriented subjects’ attention to locations in WM.

It is important to note that in our experiment the number of objects and features fell within the limits of WM capacity (c.f. Wheeler & Treisman, 2002; Vogel et al., 2001; Luck & Vogel, 1997). It is possible that the findings may have been different if the number of objects or features in the perceptual array was beyond the capacity of WM. When arrays exceed WM capacity, internal representations of arrays may be insufficient to afford selection by retro-cues. In these cases, pre-cues may bias significantly the perceptual processing of the array in order to confer behavioral advantages. Further experimentation is needed to clarify this issue.

The finding of a similar pattern of behavioral benefits and costs for pre-cues and retro-cues suggests that a reasonable representation of the array was available after a neutral pre-cue in the retro-cue trials, otherwise retro-cues would not show the same pattern of effects as pre-cues. This suggests that the enhancement of early perceptual representations is not necessary to drive the behavioral benefits and costs of attention in the current study. The results are compatible with a weighted integration and data-limited view of attention as proposed by Kinchla et al. (1995), in which more weight is given to cued elements in an internal representation with regard to response selection. Alternatively, it is possible that retro-cues act to enhance portions of the internalized representation of the array. As both accuracy and reaction-time data showed the same pattern of results, they rule out explanations based on speed/accuracy tradeoffs.

One shortcoming of the design in Experiment 1, which limits interpretations of the results, is that it is not possible to know which array location(s) the subjects used to make a decision about the presence or absence of the probe stimulus from the array. This leaves open the possibility that subjects adopted different response criteria for cued and uncued locations in the array, as they knew the probe was more likely to have appeared at the cued location. Validity effects could therefore have been contaminated by differences in response criteria for probes that occurred at cued versus

uncued locations—an effect that would be expected to be similar for both pre-cue and retro-cue trials.¹

EXPERIMENT 2: PREDICTING LOCATIONS IN EXTERNAL VERSUS INTERNAL SPACE (PERIPHERAL PROBES)

In a follow-up experiment, we presented the probe stimulus peripherally, at one of the four original array locations. The probe required a decision to be made about the item that had occurred at a specific spatial location of the array. Subjects decided whether the color of the probe and the item at the same location in the array matched (50% probability). Behavioral differences between valid, neutral, and invalid trials using these peripheral probes are not affected by differential response criteria for different array locations, since decisions are probed at each location separately. As before, the pre-cue and retro-cue stimuli did not afford any response decisions. Rather, they predicted (80% validity) the likely location to be probed.

The results established that the behavioral effects of orienting to locations in both extrapersonal space and internal representations observed in Experiment 1 were not due to differences in response criteria between valid and invalid trials.

Results

Subjects were able to perform both pre-cue and retro-cue trials while maintaining visual fixation. Analysis of eye movements indicated a minimal number of deviations from central gaze (an average of six trials per subject were rejected).

Reaction Times

The pattern of reaction-time results is shown in Figure 3A. The first comparison was between valid and invalid trials for pre-cues and retro-cues. There was a significant main effect of validity, $F(1,9) = 207.155, p < .001$, reflecting shorter reaction times in valid trials. There was no effect of cue, or interaction between cue and validity. This indicates that the pattern of shortened reaction times for valid versus invalid trials was equivalent for pre-cues and retro-cues.

Reaction-time advantages for valid pre-cues and retro-cues relative to neutral cues were tested using a two-way repeated-measures ANOVA with factors of response (yes, no) and cue (pre, retro, neutral), using only valid pre-cue and retro-cue trials. There was a main effect of cue, $F(2,18) = 56.660, p < .001$, indicating differences in reaction times between the three conditions. Post hoc contrasts revealed that neutral trials had longer reaction times than both pre-cue and retro-cue trials [pre-cue vs. neutral, $F(1,9) = 39.305, p < .001$; retro-cue vs. neutral, $F(1,9) = 65.861, p < .001$]. Reaction times in pre-cue

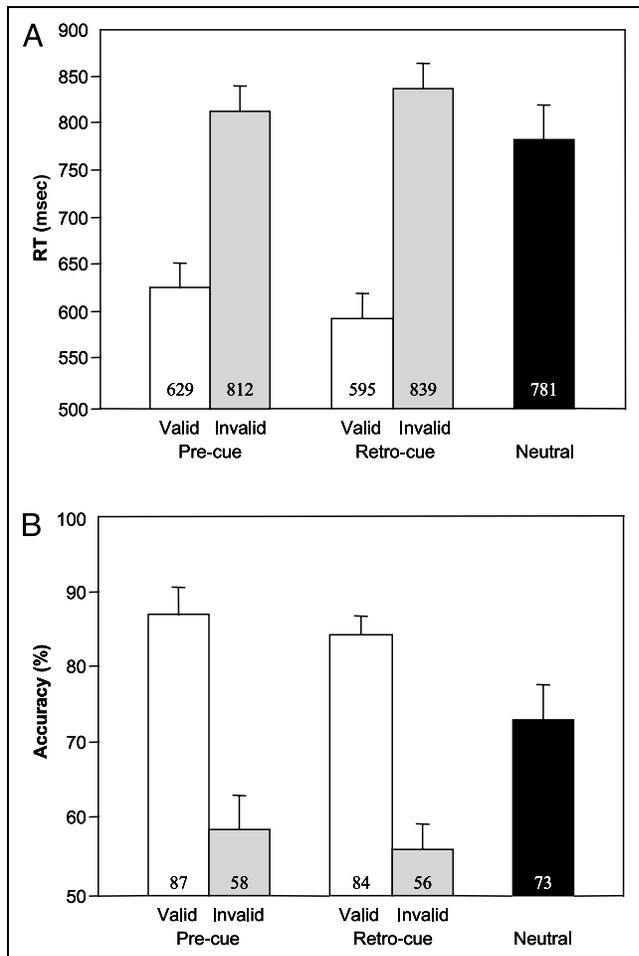


Figure 3. (A) Experiment 2: Mean reaction time (RT) and standard error for probe stimuli in pre-cue, retro-cue, and neutral trials, separated according to the factor of cue validity. “Yes” and “no” trials have been collapsed. (B) Experiment 2: Mean accuracy and standard error for probe stimuli in pre-cue, retro-cue, and neutral trials, separated according to the factor of cue validity. “Yes” and “no” trials have been collapsed.

trials versus retro-cue trials were equivalent. There was a main effect of response, $F(1,9) = 49.572, p < .001$, reflecting quicker responses to probe stimuli that matched the item that had been present at the probed location in the array (“yes” probes). There was also a significant interaction between the response and cue factors, $F(2,18) = 4.181, p = .047$. Post hoc contrasts revealed that the differences in reaction time between “yes” and “no” trials were larger for pre-cue and retro-cue trials compared to neutral trials (although the effect in retro-cue trials only tended toward significance) [pre-cue/neutral \times yes/no, $F(1,9) = 5.860, p = .039$; retro-cue/neutral \times yes/no, $F(1,9) = 4.876, p = 0.055$]. There was no difference between pre-cue and retro-cue trials.

Reaction-time costs for invalid pre-cues and retro-cues relative to neutral cues were tested using a similar analysis with factors of response (yes, no) and cue (pre, retro, neutral), using only invalid pre and retro-cue trials. There were no significant effects of cue, or

interaction between cue and response. There was only a significant main effect of response, $F(1,9) = 7.098$, $p = .026$, again indicating shorter reaction times to probe stimuli that matched the item that had been present at the probed location in the array (“yes” probes).

Accuracy

The pattern of performance accuracy in the experimental conditions is shown in Figure 3B. The first comparison was between valid and invalid trials for pre-cues and retro-cues. There was a significant main effect of validity, $F(1,9) = 105.498$, $p < .001$, reflecting greater accuracy in valid trials. There was no effect of cue, or interaction between cue and validity. This indicates that the pattern of increased accuracy for valid versus invalid trials was equivalent for pre-cues and retro-cues.

Accuracy advantages for valid pre-cues and retro-cues relative to neutral cues were tested using a two-way repeated-measures ANOVA with factors of response (yes, no) and cue (pre, retro, neutral), using only valid pre-cue and retro-cue trials. There was a main effect of cue, $F(2,18) = 7.580$, $p = .011$, indicating differences in accuracy between the three cue types. Post hoc contrasts revealed that neutral trials had less accuracy than both pre-cue and retro-cue trials [pre-cue vs. neutral, $F(1,9) = 9.076$, $p = .015$; retro-cue vs. neutral, $F(1,9) = 7.839$, $p = .021$]. Accuracy in pre-cue trials versus retro-cue trials was equivalent. There was no significant effect of response, indicating no differences in accuracy between “yes” and “no” trials. There was a significant interaction between response and cue, $F(2,18) = 4.414$, $p = .049$. Post hoc contrasts revealed that the interaction was due to the differences in accuracy between “yes” and “no” trials being greatest for pre-cue trials compared to neutral trials [pre-cue/neutral \times yes/no, $F(1,9) = 5.170$, $p = .049$].

Accuracy costs for invalid pre-cue and retro-cue trials relative to neutral cues were tested using a similar analysis with factors of response (yes, no) and cue (pre, retro, neutral), using only invalid pre- and retro-cue trials. There was a main effect of cue, $F(2,18) = 23.580$, $p < .001$, indicating differences in accuracy between the three cue types. Post hoc contrasts revealed that neutral trials had greater accuracy than both pre-cue and retro-cue trials [pre-cue vs. neutral, $F(1,9) = 35.906$, $p < .001$; retro-cue vs. neutral, $F(1,9) = 24.656$, $p = .001$]. Accuracy in pre-cue trials versus retro-cue trials was equivalent. There was no significant effect of response, or interaction between cue and response.

Summary

The pattern of results in Experiment 2 was almost identical to those observed in Experiment 1. Subjects

had decreased reaction times and increased accuracy in valid trials compared to invalid trials. Compared to neutral trials, subjects showed reaction time and accuracy advantages for valid trials, and accuracy disadvantages for invalid trials. These reaction time and accuracy effects were equivalent for pre-cues and retro-cues. Overall, reaction times were shorter for trials where the probe stimulus matched the item that had been present at the probed location in the array (“yes” probes) compared to trials where it did not match the item that had been present at the probed location in the array (“no” probes) for all cue types (pre-cue, retro-cue, neutral).

Discussion

The aim of Experiment 2 was to replicate the behavioral benefits and costs of orienting attention to upcoming perceptual stimuli and internal representations, using a modified version of the task in Experiment 1 that controlled for possible differences in response criteria between cued and uncued array locations. We showed that in this task there were behavioral effects associated with pre-cues and retro-cues that were almost identical to those seen in Experiment 1.

The finding of similar behavioral costs and benefits of pre-cues and retro-cues in Experiment 2 ruled out changes in response criteria as the only explanation for the effects. Presentation of the probe stimulus at one of the four array locations meant that a decision about the presence or absence of the probe had to be made at only one location. Therefore, any differences in performance between valid and invalid trials cannot be attributed to subjects adopting different response criteria for cued and uncued locations in the array when making their decision about the presence or absence of the probe stimulus. The results from Experiment 2 suggest a spatially specific enhancement of portions of the internal representation of the stimulus array.

The behavioral results from Experiments 1 and 2 thus demonstrate that we are able to orient selectively to spatial locations within internal spatial representations as well as to external perceptual stimuli, with these effects not being due to differences in response criteria between valid and invalid trials. However, one cannot determine whether the same or different processes underlie these effects in the two cases by behavioral measures alone. ERPs provide a measure of on-line information processing during task performance.

EXPERIMENT 3: IMPERATIVE CUEING OF EXTERNAL VERSUS INTERNAL SPACE

Data from 12 subjects (7 men) were used to characterize the behavioral and ERP effects of cueing attention to

perceptual locations and internal representations. The same 12 subjects were used for both behavioral and ERP analysis. Data were rejected from 7 additional subjects due to excessive eye blinks or saccades, and from 5 additional subjects who had excessive artefacts during EEG recording.

Results

Behavioral Results

The pattern of reaction times is shown in Figure 4A. There was no significant effect of cue, or interaction between cue and response, indicating that the pattern of results was equivalent for pre-cues and retro-cues. There was a significant main effect of response, $F(1,11) = 60.577, p = .0001$, reflecting faster responses to probes that occurred in the cued location than probes that were not in the cued location. These two results, faster “yes” responses than “no” responses, and no differences

between pre- and retro-cues, mirror those found in Experiments 1 and 2.

The pattern of accuracy is shown in Figure 4B. There was no significant effect of cue, or interaction between cue and response. There was a significant main effect of response, $F(1,11) = 18.691, p = .001$, reflecting more accurate responses to probes that occurred at the cued location than to probes that were not in the cued location. As with the reaction-time data, the increased accuracy for “yes” responses compared with “no” responses, and the absence of differences between pre-cues and retro-cues, are similar to the findings from Experiments 1 and 2.

ERP Results

Waveforms to the spatial cues were characterized by early visual responses over lateral posterior sites and a late positive peak broadly distributed over the scalp. Experimental factors exerted three types of effects upon waveforms elicited by spatial cues: effects of spatial orienting that were common for pre-cues and retro-cues, effects of spatial orienting that were selective for either pre-cues or retro-cues, and effects of cue (pre, retro) that were independent of the direction of attention (left, right).

Common effects of spatial orienting for pre-cues and retro-cues. Common effects of spatial orienting were calculated as effects of side of attention that did not interact with cue type. Pre-cues and retro-cues elicited a common set of lateralized posterior and frontal ERP components sensitive to the direction of attention. There was an early modulation of the visually evoked N1 component over the posterior scalp contralateral to the direction of attention (see Figures 5 and 6). Statistically, this effect was evident at the posterior and lateral scalp regions between 120 and 200 msec, as both two-way interactions between side of attention and hemisphere, and three-way interactions between side of attention, hemisphere, and electrode site, $F_s > 5.274, p < .01$. These reflect the fact that the N1 was enhanced over the right hemisphere when subjects attended left, and over the left hemisphere when subjects attended right, and that these effects were maximal at the PO7/8 and TP7/8 electrode pairings. They also reflect the fact that this contralateral N1 enhancement was larger over the left hemisphere.

A later common effect of spatial orienting involved a contralateral central and frontal negativity between 360 and 480 msec (see Figures 5 and 6). Statistically, these effects were evident over frontal, central, and lateral scalp regions as two-way interactions between direction of attention and hemisphere, and three-way interactions between direction of attention, hemisphere, and electrode site, $F_s > 2.713, p < .05$. These interactions with electrode site indicate that the differences were maximal at the F5/6, C3/4, and FC5/6 electrode pairs.

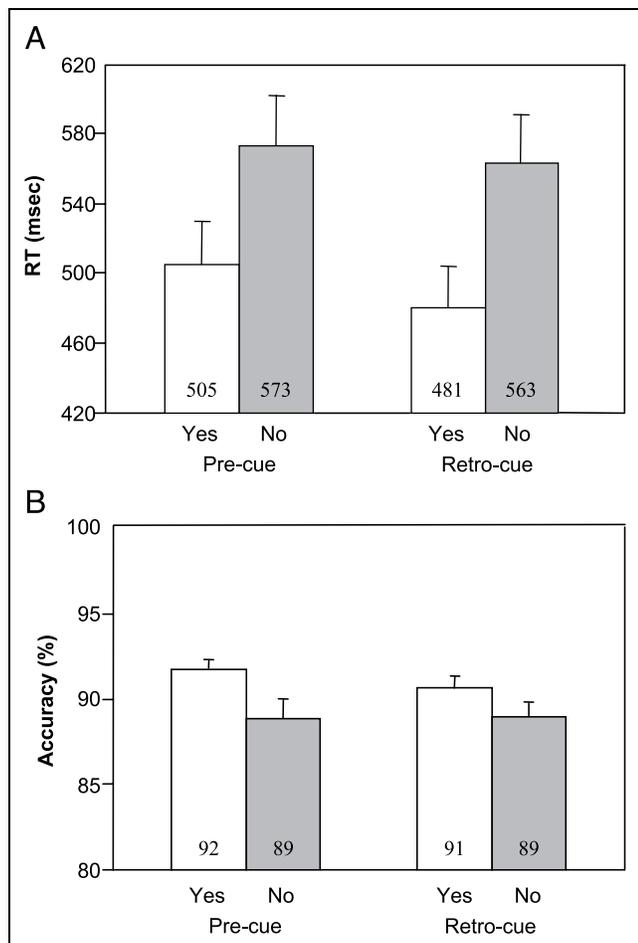
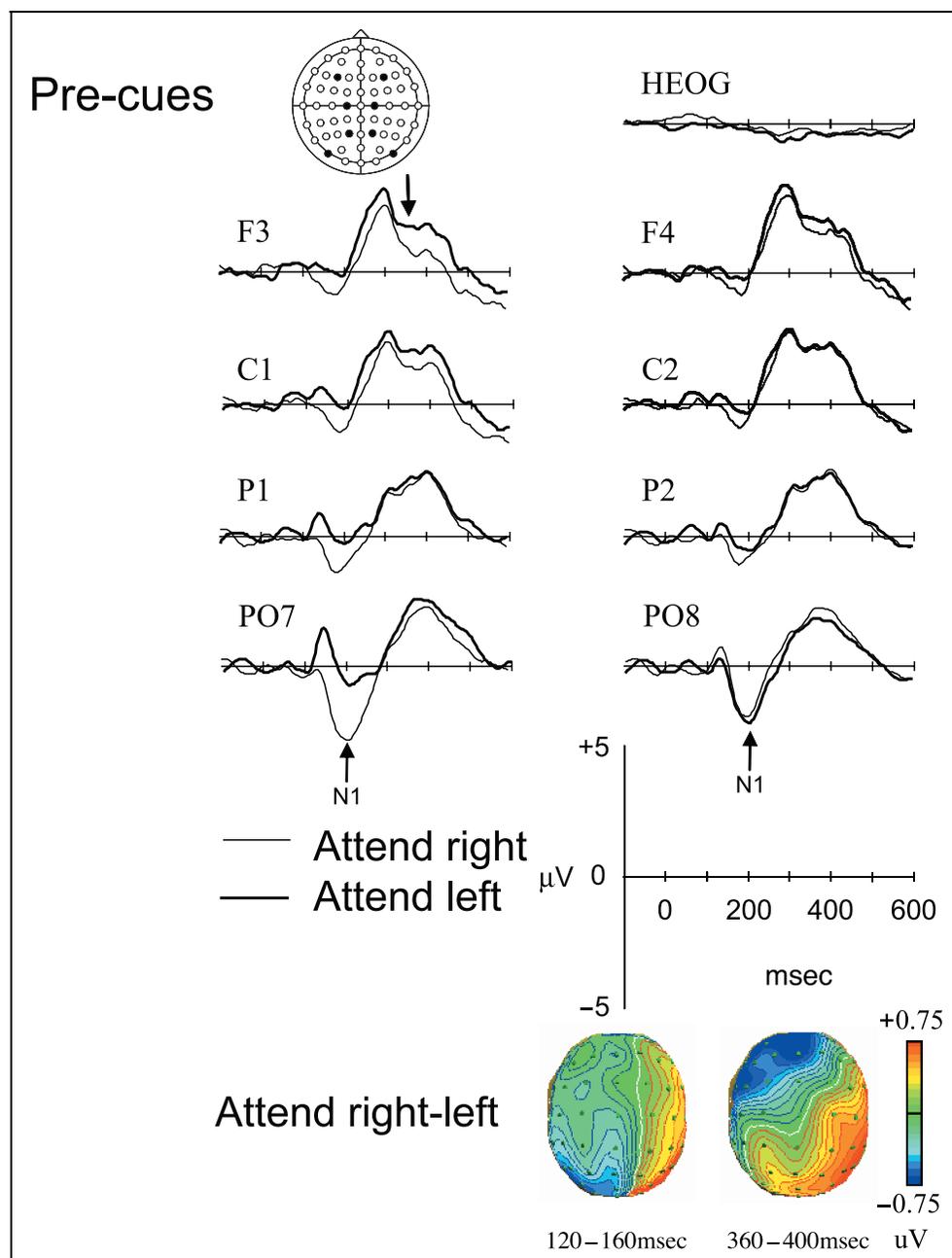


Figure 4. (A) Experiment 3: Mean reaction time (RT) and standard error for probe stimuli in pre-cue and retro-cue trials, separated according to the factor of response. (B) Experiment 3: Mean accuracy and standard error for probe stimuli in pre-cue and retro-cue trials, separated according to the factor of response.

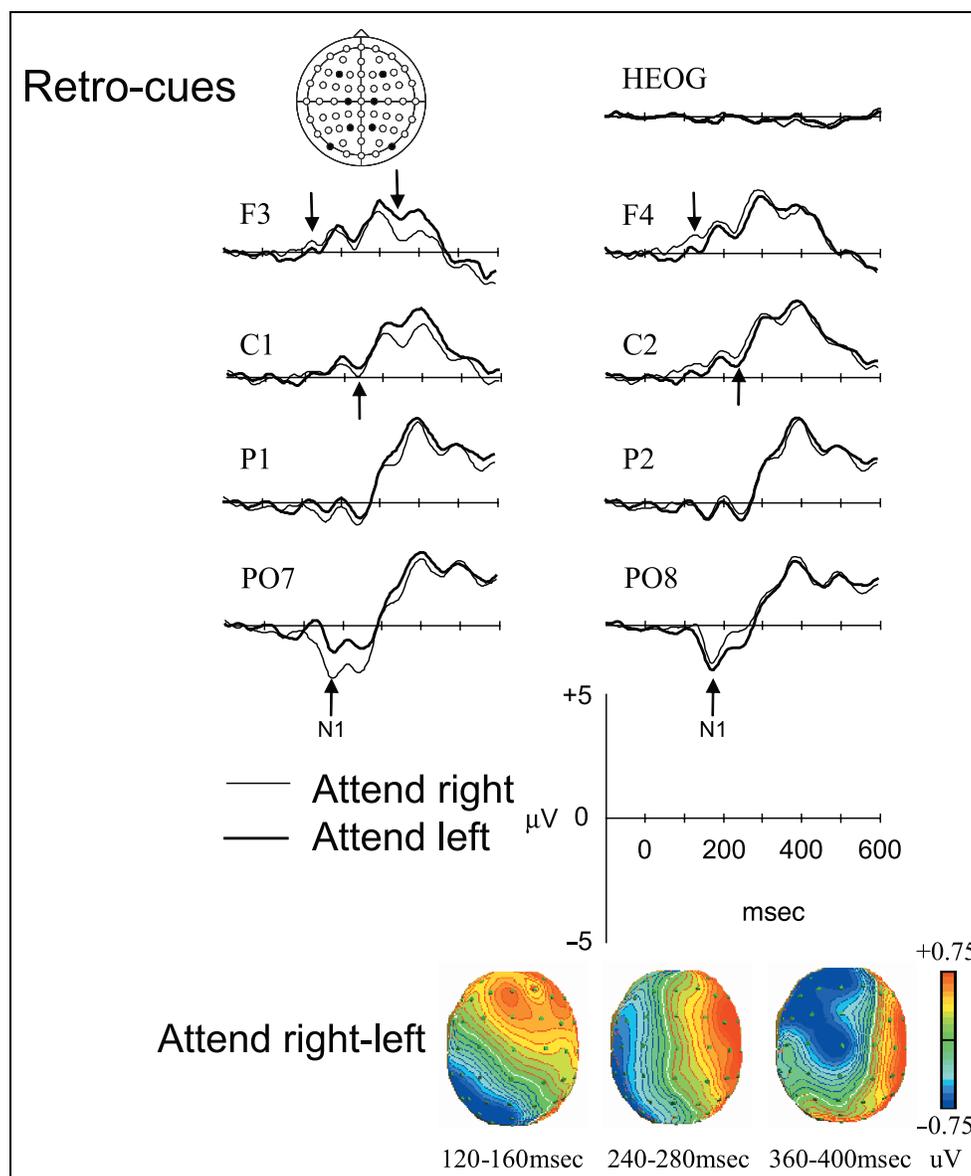
Figure 5. Grand-averaged waveforms ($N = 12$ subjects) elicited by pre-cue stimuli when subjects attended the left (thick line) and right (thin line) visual fields. To isolate effects of spatial orienting, both attend-left and attend-right waveforms have had the waveform from the neutral cue stimulus that occurred at the same time point subtracted from them. The electrode montage is shown at the top-left, with the locations of the electrode sites for the sample waveforms shaded black. The horizontal eye channel (HEOG) is also shown. The polarity of the waveforms is plotted with positive values upward, and arrows indicate the presence of statistically significant effects in this and subsequent figures. Scalp topographies of the difference in grand-averaged ERPs elicited by pre-cue stimuli when subjects attended the right versus left visual fields are shown at the bottom of the figure. The maps are shown from a bird's-eye perspective. The color scale (colored bar on the right) shows the range of possible voltage values in the topographies. The anterior scalp is shown at the top and the right scalp is shown at the right side in this and subsequent figures.



Effects of cue independent of the direction of attention. Differences between orienting to perceptual versus internal representations were revealed by effects of cue that did not interact with side of attention. Differences during the P300 component were observed between pre-cues and retro-cues. There was an increased relative positivity for retro-cues over posterior scalp regions, and an increased relative negativity for retro-cues compared with pre-cues over the anterior scalp (see Figure 7). This effect was nonlateralized, and was evident from 360 msec onwards as both a main effect of cue, and interaction between cue and electrode site over mid-line, frontal, central, lateral, and posterior scalp sites, $F_s > 3.578$, $p < .046$.

Selective effects of spatial orienting for retro-cues. Differences in lateralized spatial orienting between pre-cues and retro-cues were revealed by statistical interactions between the factors of direction of attention (left, right) and cue (pre, retro). The first such interaction occurred early, between 120 and 200 msec, over the frontal scalp sites. Modulation of ERPs was only present for retro-cues, and was a difference in the waveforms over the anterior scalp regions. There was an increased relative positivity over these regions when subjects attended right (see Figure 6). This was reflected by interactions between direction of attention and cue over frontal [120–200 msec; $F_s > 8.803$, $p < .013$] and central regions [160–200 msec; $F(1,11) = 5.953$,

Figure 6. Grand-averaged waveforms ($N = 12$ subjects) elicited by retro-cue stimuli when subjects attended the left (thick line) and right (thin line) visual fields. To isolate effects of spatial orienting, both attend-left and attend-right waveforms have had the waveform from the neutral cue stimulus that occurred at the same time point subtracted from them. Scalp topographies of the difference in grand-averaged ERPs elicited by retro-cue stimuli when subjects attended the right versus left visual fields are shown at the bottom of the figure.



$p = .033$]. During this time period, there was also a main effect of cue over the frontal scalp sites [160 and 200 msec; $F(1,11) = 15.039$, $p = .003$]. Retro-cues evoked a positive potential, which was not evident for pre-cues (see Figure 7).

A later effect was only present for retro-cues, and was a difference in the relative negativity/positivity between the two hemispheres depending on the direction of attention between 240 and 320 msec over frontal, central, and lateral scalp sites (see Figure 7). This was evident both as two-way interactions of cue and hemisphere, and three-way interactions between cue, side of attention, and hemisphere, F 's > 6.139 , $p < .031$. These indicate that for retro-cues, when attention was directed to the right, the distribution of negative charge was greater over the left hemisphere, and the distribution of positive charge was greater over the right hemisphere.

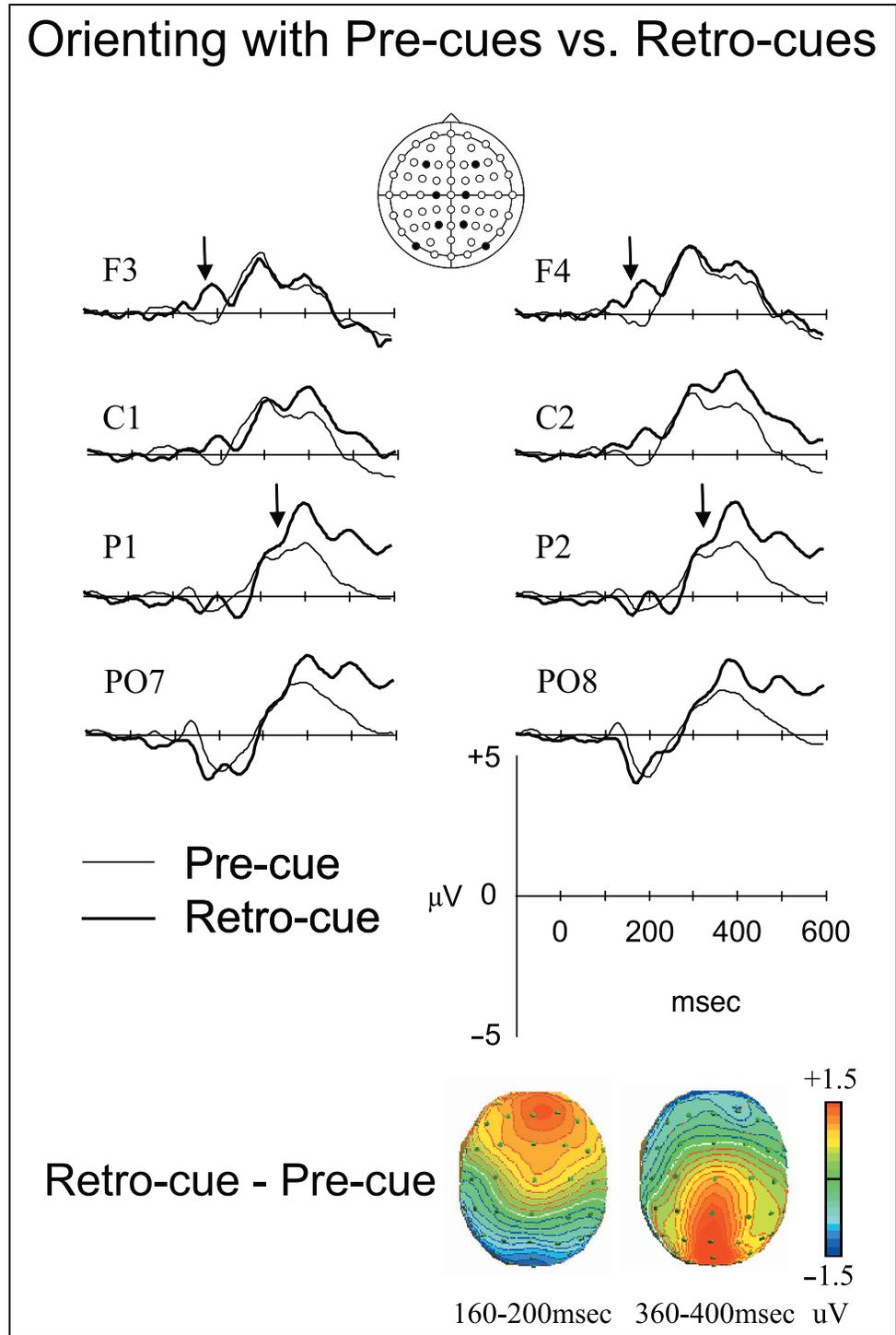
Discussion

ERP recordings during task performance permitted real-time measurement of the orienting of attention by identical cueing stimuli to a location in an upcoming perceptual array, or to the same location in the internal representation of the array. The neural correlates of the two processes share a common pattern of lateralized activity over the posterior then frontal regions. Additional processes including early frontal activity are involved when orienting toward a representation in WM.

Behavioral Results

Behavioral results from Experiment 3, which used imperative, as opposed to predictive cues, were compatible with those seen in Experiments 1 and 2. Subjects were faster, and more accurate, to respond when probe stimuli had

Figure 7. Grand-averaged waveforms ($N = 12$ subjects) elicited by pre-cue stimuli (thin line) and retro-cue stimuli (thick line). To isolate effects of spatial orienting, both pre-cue and retro-cue waveforms have had the waveform from the neutral cue stimulus that occurred at the same time point subtracted from them. Scalp topographies of the difference in grand-averaged ERPs elicited by retro-cue stimuli versus pre-cue stimuli are shown at the bottom of the figure.



occurred in the cued location (“yes” responses) than when it had occurred at an uncued location. Once again, there was no difference in the pattern of results between the pre-cue and retro-cue conditions.

ERP Results

The analysis of the ERPs elicited by the cueing stimuli revealed that there were both similarities and differences in the attentional mechanisms involved in the

optimization of behavior by pre-cues and retro-cues. The task equated perceptual and motor demands between the two conditions. Analysis was carried out on physically identical cueing stimuli occurring either before or after the array. Because pre-cues and retro-cues occurred after different types of events and at different stages in a trial, direct comparison of their waveforms might have reflected differential overlap from preceding events or differential cognitive states that were not linked to spatial orienting. Therefore, to

minimize contribution from these nonspecific factors, we subtracted the waveforms elicited by neutral cue stimuli from those elicited by informative cues that occurred at the same time point. To minimize further possible contribution from differential component overlap from preceding items, intervals between successive trial events were randomly jittered. Only the effects of spatial orienting before or after the array are therefore captured in the resulting waveforms considered in the analysis.

Common processes in pre-cue and retro-cue trials. Attentional orienting modulated the contralateral visual N1 component in both pre-cue and retro-cue trials. Contralateral negativities have been reported in most previous studies of attentional orienting (Hopf & Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994; Harter et al., 1989) although none of the effects began as early as ours (120 msec). Such effects have been interpreted as reflecting the initial steps of attentional orienting toward a spatial location. There were physical differences in the cueing stimuli for attending left and right in this study (and some of the others), which may have contributed to the earliest parts of the effect. However, the fact that similar early negativities were found when stimuli were physically equated across cueing conditions (Nobre et al., 2000), suggests that the N1 modulation may reflect part of the process of orienting visual attention. Given that the same effect was found in pre-cue and retro-cue trials, this suggests that some early stages of orienting to spatial locations and mental representations may share the same underlying processes. However, the existence of purely attentional early contralateral modulation has been challenged recently by Velzen and Eimer (submitted), who found that N1 modulation depended on physical asymmetries of the predictive properties of central cue stimuli. Further investigation will be required to clarify this important issue.

Inspection of waveforms revealed that the N1 modulation was much larger over the left hemisphere. Larger left hemisphere differences were also seen for the early negativities in other orienting studies (Hopf & Mangun, 2000; Nobre et al., 2000). Initially, this does not seem consonant with the notion of right hemisphere specialization for directing attention (Mesulam, 1981). However, this may indicate that there was greater variability in the activity in posterior left hemisphere regions between directing attention to the left and right, whereas the right hemisphere was more similarly involved in attention shifts in both directions (c.f. Nobre et al., 2000). This is consistent with behavioral, lesion, and imaging data that have suggested that right hemisphere regions are able to direct attention into both visual hemifields, while posterior left hemisphere regions are primarily involved in directing attention into the right hemifield (Mesulam, 1981, 1999).

Also common to pre-cues and retro-cues were effects sensitive to the direction of attentional orienting be-

tween 360 and 480 msec. There was increased relative negativity over fronto-central left hemisphere sites when attention was directed to the right. Late frontal activity has been consistently reported in studies of shifting spatial attention (Hopf & Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994; Harter et al., 1989), however, its distribution and polarity have varied between these studies. The precise neural processes responsible for these effects, and the reason for their variability between tasks, remain to be understood.

Late positive potentials over posterior scalp sites linked to directing attention (LDAP) have frequently been reported in spatial attention experiments (Eimer, Velzen, & Driver, 2002; Hopf & Mangun, 2000; Harter et al., 1989). The possible contribution of this potential could not be evaluated in the present experiment because of the restricted time window analyzed after each cue stimulus. The occurrence of probe stimuli at a relatively short time period after retro-cues (500–1000 msec) precluded the measurement of uncontaminated cue-related activity during the late time intervals associated with the LDAP. In future experiments, it will be interesting to extend the interval between retro-cues and probes in order to examine whether this component is elicited when orienting to internal representations.

Selective effects of spatial orienting for retro-cues. In the retro-cue condition only, there was modulation of activity depending on cue direction (left, right) over frontal scalp sites between 120 and 200 msec. The earliest reported frontal effects in attentional orienting tasks have begun at 200 msec (Nobre et al., 2000), and no effects as early as this have been seen in studies where subjects are cued to retrieve spatial or object information from WM (Bosch et al., 2001; Mecklinger, 1998). Awh et al. (2000) found early modulation of activity over frontal scalp sites to probe stimuli by both spatial attention and rehearsal in WM in a task where subjects either had to attend to, or remember, spatial locations. However, this effect, unlike the present finding, was not restricted to the memory condition. The present finding of early frontal modulation appears to be specific to orienting to internal mental representations.

The most intuitive explanation of the current results would be selective engagement of frontal regions when orienting to mental representations in WM. There is an enormous literature about frontal involvement in WM (e.g., Levy & Goldman-Rakic, 2000; Owen, 2000; Petrides, 2000), and it is possible that the present effect, being restricted to retro-cues, reflects some aspect of orienting to internal representations. Its early latency is consistent with a source of stimulus-driven top-down biasing signal (Desimone & Duncan, 1995), that could perhaps guide the retrieval, maintenance, or filtering of information within WM. Its latency makes it less likely to reflect later monitoring or decision-related processes. However, the exact functional significance of this effect remains to be resolved. It has been suggested (Vogel & Luck, 2000)

that such early frontal effects in some cases may reflect overlap with motor potentials linked to response preparation. This is unlikely here, as the response decision is not afforded until the probe stimulus is presented.

As this early frontal effect temporally overlaps with the posterior N1 modulation, this suggests that concurrent activity in multiple brain areas underlie the observed effects. Although it is hard to pinpoint the sources of these modulations, it is possible that they may be related, as studies have shown interactions between frontal and parietal areas during WM tasks (e.g., Chafee & Goldman-Rakic, 2000). What can be concluded is that brain activity reflected over frontal scalp regions plays an early role in orienting attention to internal representations.

The next phase of differences restricted to retro-cues were hemispheric differences in the distribution of positive and negative charge depending on cue direction over frontal, central, and lateral scalp sites between 240 and 320 msec. Although frontal and central modulations dependent on the direction of attention were seen in attentional orienting studies (Hopf & Mangun, 2000; Nobre et al., 2000) around this time period, the fact that here they were only present for retro-cues suggests an explanation based more on spatial WM than on attention. Possible contributory processes include interactions between biasing signals and extrastriate regions (Desimone & Duncan, 1995), maintenance or retrieval of spatial information from WM, target selection, and filtering of distractors. The wide distribution of the effect (as opposed to only frontal scalp sites) suggests the activity of a distributed network(s) of brain areas, perhaps engaged in multiple temporally overlapping functions.

The final difference between pre-cues and retro-cues was enhancement of the P300 component for retro-cues. The P300 component can be modulated by many factors, although in this case we believe that the enhanced positivity for retro-cue trials reflected the context updating or closure of the selection process (Donchin & Coles, 1988; Desmedt, 1980). This is because informative retro-cues defined both the stimulus location and the stimulus color to be selected, as the stimulus array had already been presented. In contrast, informative pre-cues provide information about the location, but not the color to be selected. Color information is deferred until array presentation. Therefore, the enhanced P300 to retro-cues could reflect increased closure of the selection process.

Neural systems for spatial orienting to external and internal space. Convergent findings from neuropsychology, brain imaging, and primate studies have shown that visual spatial orienting toward extrapersonal space involves a large-scale network of parietal and frontal cortical areas (see Nobre, 2001; Mesulam, 1999 for reviews). ERPs elicited by cues that direct attention to spatial locations consistently show early lateralized modulation over posterior parietal scalp locations followed

by lateralized modulation over anterior scalp locations (Hopf & Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994; Harter et al., 1989). This pattern of ERP modulation is consistent with parietal and frontal activation during the spatial orienting of attention, and tentatively suggests that parietal activity leads frontal activity in the control of spatial attentional orienting (c.f. Velzen & Eimer, submitted).

The present results suggest that orienting spatial attention to external and internal spatial locations both involve this same network reflected in parietal–frontal ERP modulations. Furthermore, orienting attention to locations in internal representations engages additional processes, including early processing reflected over the frontal scalp and widely distributed changes in later ERP components. These results are consistent with findings from a recent fMRI investigation of spatial orienting to external versus internal spatial representations (Nobre et al., 2002). The task was similar to Experiment 3, except that the intervals between successive displays were much longer, in order to resolve the brain activity related to cues and arrays separately. Both pre-cues and retro-cues engaged activity in the core posterior parietal, lateral premotor, and dorsal prefrontal areas of the spatial orienting network. In addition, retro-cues selectively engaged more anterior prefrontal areas and enhanced common activations in the parietal cortex. The present ERP results suggest that the prefrontal contribution, selectively linked to orienting spatial attention to internal representations, may occur quite early in the orienting process. Early prefrontal involvement would be in line with a top-down role in controlling attentional selection guided by memory.

Complementary findings in other studies. Our results are consistent with reports of the shared action of attention and WM upon visual processing. Awh and colleagues (2000) found that both spatial attention and rehearsal in spatial WM modulated early visual-evoked potentials and frontal activity to probe stimuli in a task where subjects either had to attend to, or remember, spatial locations. This gave support to the suggestion that information is maintained in spatial WM by focal shifts of spatial attention (e.g., Awh, Jonides, & Reuter-Lorenz, 1998; Awh & Jonides, 2001). In another study, pre-cues directed subjects' attention to a location in a stimulus array, and post-cues probed whether a target was present at the pre-cued location (Luck et al., 1994). P1 and N1 modulation of these post-cue stimuli occurred as a function of pre-cue validity, similarly suggesting attentional enhancement of relevant locations in WM. However, these findings are not directly comparable to the current study, as they reflect the modulatory effects of spatial attention to a location probed by a peripheral post-cue stimulus, rather than analysis of cues that initiate spatial orienting toward locations in internal representations. Here we extend

the view that attention and WM can have similar effects on stimulus processing by showing that the orienting processes to perceptual stimuli and stimuli in mental representations can also share similarities.

Our results also complement findings of a strong relationship between perceptual functions and mental imagery (cf. Kosslyn et al., 2001; Ishai et al., 2000). In our task, retro-cue trials are likely to involve mental imagery of the remembered array. Of interest is the finding of enhanced posterior negativity in the N1 time range (150–200 msec) to letter stimuli if they match the letter subjects hold as a mental image, compared to when they are imagining a different letter (Farah, Peronnet, Gonon, & Giard, 1988). The authors suggested that mental imagery might involve stimulus representations in the visual system. Findings of similar areas of activation during imagery and perception (e.g., Kosslyn et al., 2001; Ishai et al., 2000; O'Craven & Kanwisher, 2000), as well as the behavioral effects of imagery upon perceptual performance (Pashler & Shiu, 1999; Ishai & Sagi, 1995; Farah, 1985), support this view. Our findings of similar early processes in both pre-cue and retro-cue trials are consistent with the view that attention to mental imagery and perception may share similarities. The additional activity seen in retro-cue trials may in some way be related to mental imagery, the accessing of perceptual information from memory.

Summary. In conclusion, we have demonstrated that it is possible to orient selective spatial attention to internal representations when within WM capacity. Orienting attention to internal representations was characterized by an equivalent pattern of behavioral costs and benefits as orienting to spatial locations across three experiments. These validity effects were not due to changes in response criteria. They may have reflected spatially specific enhancement of representations and/or increased weighting given to spatially attended stimuli for response selection. ERP analysis of the identical cueing stimuli revealed that the neural correlates of the two processes shared both similarities and differences. Orienting spatial attention to both perceptual locations and internal representations involved lateralized activity over posterior, and then frontal regions, as has been seen in previous studies of attentional orienting. Additional processes, including early activity over frontal scalp sites, are involved when orienting attention to an internal representation held in WM.

METHODS

Experiment 1: Predicting Locations in External Versus Internal Space

Subjects

Ten healthy right-handed (Oldfield, 1971) subjects (age range 21–36 years, 6 women) took part in the experiment as paid volunteers. All participants reported being

free of neurological disorders. Visual acuity was normal or corrected to normal.

Stimuli and Task

The task is illustrated in Figure 1A. Participants viewed arrays of four differently colored crosses either preceded or followed by spatial cues, and made a delayed decision about the color of the items in the array. There were three types of trial: pre-cue, retro-cue, and neutral trials. The key difference between the trial types was whether and when in the trial the attentional orienting cue was presented. In pre-cue trials, a spatially informative cue (80% validity) was presented 1500–2500 msec before the visual array of colored crosses. In retro-cue trials, the spatially informative cue (80% validity) was presented 1500–2500 msec after the array. In neutral trials, there was no spatially informative cue, either before or after the array. Each trial contained the same sequence of events. Firstly, an asterisk was presented at the center of the screen (200 msec), which indicated the start of the trial. A square (side length 0.8°) then appeared at the center of the screen.

After an interval that ranged randomly from 400 to 600 msec, a pre-cue was presented for 100 msec. The pre-cue was informative in pre-cue trials, but neutral in retro-cue and neutral trials. An informative cue consisted of two adjacent sides of the square brightening (forming an arrow), which instructed the subject to attend covertly to that position (e.g., top left). Neutral cues consisted of the whole square brightening, which gave no spatial information. After a random interval varying between 1500 and 2500 msec, an array of four crosses of different colors appeared for 100 msec. The crosses were any four of the following colors: red, blue, green, yellow, orange, cyan, pink, gray. Each cross was 0.8° visual angle in size, and centered at 3° horizontal and 3° vertical eccentricity. After another random delay, ranging between 1500 and 2500 msec, a retro-cue was presented for 100 msec. The retro-cue was informative in retro-cue trials, but neutral in pre-cue and neutral trials. The informative cue again consisted of two adjacent sides of the square brightening (forming an arrow), which instructed the subject to attend covertly to that location in the internal mental representation of the array (e.g., bottom left). Neutral cues again consisted of the whole square brightening, which gave no spatial information. After a random interval between 500 and 1000 msec, a colored cross (any one of the eight possible colors; probe stimulus) was presented at the center of the screen for 100 msec. The task was to decide whether the probe stimulus was present or absent from the array. When the probe stimulus had been present in the array, the informative pre-cues and retro-cues predicted its correct location 80% of the time. Subjects responded by pressing the left button of the response box if the probe stimulus did appear in the array, and the right button if the probe stimulus did not appear in the array.

The probe stimulus was present or absent with equal (50%) probability. This was true for pre-cue, retro-cue and neutral trials. All trial types occurred in a random order throughout the experiment. There were 352 trials in total (160 pre-cue, 160 retro-cue, 32 neutral). Of the pre-cue trials, 64 were valid (stimulus was in the array, at the cued location), 16 were invalid (stimulus was in the array, at an uncued location), and 80 contained a probe stimulus that was not in the array. Retro-cue trials contained the same ratio of experimental conditions. Of the neutral trials, 16 contained a probe that was in the array, and 16 contained a probe that was not in the array. There were 12 blocks of trials in the experiment, plus one additional practice block at the beginning.

Procedure

Subjects were comfortably seated in a dimly illuminated, electrically shielded room, facing a computer monitor placed 100 cm in front of them. They were informed, at the beginning of the experiment, about the relationship between the cue, array, and probe stimuli. They were asked to maintain fixation on a small cross that was continuously present at the center of the monitor. They were instructed to respond as quickly as possible following probe stimulus onset, while avoiding mistakes. Subjects responded with their right hand only.

Behavioral Analysis

Reaction times to probe stimuli and accuracy of performance were analyzed by repeated-measures ANOVAs. The first analysis compared valid and invalid trials in which the probe stimulus was present in the array. This analysis tested the factors of cue (pre, retro) and validity (valid, invalid). The second analysis tested the factors of response (yes, no) and cue (pre, retro, neutral). To evaluate benefits conferred by valid cues, only valid pre-cue and retro-cue trials were considered in this analysis. The third analysis also tested the factors of response (yes, no) and cue (pre, retro, neutral), but considered only invalid pre-cues and retro-cues, to assess any attentional costs of invalid cueing. In all analyses, post hoc contrasts were carried out to guide interpretation where appropriate.

Experiment 2: Predicting Locations in External Versus Internal Space (Peripheral Probes)

Unless stated otherwise, the methods and stimulus parameters used in Experiment 2 were identical to those in Experiment 1.

Subjects

Ten healthy right-handed (Oldfield, 1971) subjects (age range 20–36 years, 4 women) took part in the experi-

ment as paid volunteers. All participants reported being free of neurological disorders. Visual acuity was normal or corrected to normal.

Stimuli and Task

The task is illustrated in Figure 1B. As before, there were three types of trial: pre-cue, retro-cue, and neutral trials. In this experiment the probe stimulus was presented peripherally, at one of the four locations occupied by the array stimuli. The subject's task was to decide whether the probe stimulus matched the item presented at that location in the array. The informative pre-cues and retro-cues predicted the location that would be probed with 80% validity. On neutral trials the probe was equally likely to occur at any location. Subjects responded by pressing the left button of the response box if the probe stimulus did match the item at the probed location in the array, and the right button if the probe stimulus did not match the item at the probed location in the array.

As before, the probability of correct yes or no responses was equal (i.e., 50% of the time the probe stimulus was the same as the stimulus that had occurred at the probed location in the array, and 50% of the time it was different). This was true for pre-cue, retro-cue, and neutral trials. In “no” trials, the probe stimulus was randomly chosen from one of the other three colors in the array. One constraint was that in invalid trials, the probe could not be the color from the cued location. All trial types occurred in a random order throughout the experiment. There were 396 trials in total (180 pre-cue, 180 retro-cue, 36 neutral). Of the pre-cue trials, 144 were valid (the probe stimulus appeared at the cued location) and 36 were invalid (the probe stimulus appeared at an uncued location). Retro-cue trials contained the same ratio of experimental conditions. Of the neutral trials, 18 contained a probe that did match the stimulus that appeared at the probed location in the array, and 18 contained a probe that did not match the stimulus that appeared at the probed location in the array. There were 12 blocks of trials in the experiment, plus one additional practice block at the beginning.

Procedure

Eye movements and gaze position were monitored using an infrared video-based eye tracker with theoretical resolution $>0.1^\circ$ (iView, SMI). Eye movements or deviations from central fixation were detected with the eye tracker using an algorithm that calculated sites and duration of fixation points during each trial using infrared tracking. Trials with fixation points further than 1° apart from central fixation were excluded from the behavioral analysis.

Behavioral Analysis

Reaction times to probe stimuli and accuracy of performance were analyzed by repeated-measures ANOVAs, in similar fashion to Experiment 1. The first analysis compared valid and invalid trials for both pre-cues and retro-cues. This analysis tested the factors of validity (valid, invalid) and cue (pre, retro). To assess attentional benefits, the second analysis tested the factors of response (yes, no) and cue (pre, retro, neutral) using only valid pre-cue and retro-cue trials. To assess attentional costs, the third analysis also tested the factors of response (yes, no) and cue (pre, retro, neutral), but using only invalid pre-cue and retro-cue trials. In all analyses, post hoc contrasts were carried out to guide interpretation where appropriate.

Experiment 3: Imperative Cueing of External Versus Internal Space

Unless stated otherwise, the methods and stimulus parameters used in Experiment 3 are identical to those in Experiment 1.

Subjects

Twenty-four healthy right-handed (Oldfield, 1971) subjects (age range 20–31 years, 14 women) took part in the experiment. One subject participated in both Experiments 1 and 3. The experimental methods were noninvasive and had ethical approval from the Department of Experimental Psychology, University of Oxford, UK.

Stimuli and Task

The task is illustrated in Figure 1C. There were only two types of trial: pre-cue and retro-cue trials. In this experiment, the probed item was always present in the array. The subject's task was to decide whether the probe was presented at the cued location. Subjects responded by pressing the left button of the response box if the probe stimulus did appear at the cued location, and the right button if the probe stimulus did not appear at the cued location. Once again the stimulus array was made up of four differently colored crosses, however, only four possible colors were used for the array (and therefore probe) stimuli: red, blue, green, and yellow.

As before, the probability of correct yes or no responses was equal (i.e., 50% of the time the probe did occur at the cued location, and 50% of the time it did not). This was true for both pre-cue and retro-cue trials. The possible distribution of colors in the array was fully counterbalanced between response and cueing conditions. There were an equal number of trials with all the potential array types (four different colors, each in a different position). The intertrial interval varied randomly between 1500 and 1800 msec.

There were an equal number of pre-cue and retro-cue trials, and they occurred in random order throughout the experiment. To ensure enough data in all relevant conditions, subjects participated in two equivalent experimental sessions, separated by at least one week. There were 1152 trials in total over the two sessions. There were 20 blocks of trials per session, plus one additional practice block at the beginning.

Behavioral Analysis

Reaction times and accuracy were analyzed by repeated-measures ANOVAs with factors of response (yes, no) and cue (pre-cue, retro-cue).

ERP Recording

The EEG was recorded continuously from 60 scalp sites using nonpolarizable tin electrodes mounted on an elastic cap (Electro-Cap), positioned according to the 10–20 International System (AEEGS, 1991). The montage included 8 midline sites (FPZ, FZ, FCZ, CZ, CPZ, PZ, POZ, and OZ) and 26 sites over each hemisphere (FP1/FP2, AF3/AF4, AF7/AF8, F1/F2, F3/F4, F5/F6, F7/F8, FC1/FC2, FC3/FC4, FC5/FC6, FT7/FT8, C1/C2, C3/C4, C5/C6, T7/T8, CP1/CP2, CP3/CP4, CP5/CP6, TP7/TP8, P1/P2, P3/P4, P5/P6, P7/P8, PO3/PO4, PO7/PO8, and O1/O2). Additional electrodes were used as ground and reference sites. The EEG was referenced to the right mastoid, then re-referenced off-line to the algebraic average of the right and left mastoids. The signal was amplified 20,000 times and digitized at a sampling rate of 250 Hz. Data were recorded with a band-pass filter of 0.03–100 Hz. The epoching of ERPs was performed off-line. Epochs started 200 msec before and ended 600 msec after cue-stimulus onset.

Horizontal and vertical eye movements were detected by recording the horizontal and vertical electrooculogram (HEOG and VEOG) bipolarly with electrodes placed around the eyes. Eye movements were also monitored with $>0.1^\circ$ precision using an infrared video-based eye tracker (iView, SMI).

Epochs containing excessive noise or drift ($\pm 100 \mu\text{V}$) at any electrode between -200 and $+600$ msec were excluded. Epochs with eye movement artefacts (blinks or saccades) were rejected. Blinks were identified as large deflections ($\pm 50 \mu\text{V}$) in the HEOG and VEOG electrodes. Saccades or breaks in central fixation were detected with the eye tracker using an algorithm that calculated sites and duration of fixation points during each trial using infrared tracking as in Experiment 2. Trials with incorrect behavioral responses were discarded. Trials with RTs faster than 130 msec or slower than 1100 msec were regarded as errors and also excluded. To maintain an acceptable signal-to-noise ratio, subjects with fewer than 40 artefact-free trials

per condition were excluded from both behavioral and ERP analyses.

ERP Analysis

Data analysis was performed using measures of the mean voltage value (mean amplitude) over successive time bins across different scalp regions. Successive time bins in steps of 40-msec intervals between 0 and 600 msec were used. Five region-specific sets of analyses were performed over midline, frontal, central, lateral, and posterior scalp regions. The midline analysis included electrode sites FPZ, FZ, CZ, PZ, and OZ. The frontal analysis used electrodes FP1/2, AF3/4, AF7/8, F3/4, F5/6, and F7/8. The central analysis included sites FC1/2, FC3/4, C1/2, C3/4, CP1/2, and CP3/4. The lateral analysis included electrode sites FC5/6, FT7/8, C5/6, T7/8, CP5/6, and TP7/8. The posterior analysis used electrode sites: P3/4, P5/6, P7/8, PO3/4, PO7/8, and O1/2.

The main aim of the experiment was to compare the processes of orienting attention to a spatial location of an expected perceptual stimulus with orienting attention to an internal spatial representation held in WM. The analysis of ERPs therefore concentrated on comparing the spatially informative cueing stimuli that occurred before (pre-cue) or after (retro-cue) the stimulus arrays. These stimuli were physically identical, which afforded direct comparison between the two cases. Separate ERP averaged waveforms were constructed for the pre-cue and retro-cue stimuli in each direction (top-left, top-right, bottom-left, bottom right). To isolate aspects of neural activity related to attentional orienting, and to minimize the contribution of general processing differences at distinct stages of the trial, each of these conditions then had the ERP waveform for the “neutral” cue condition at the equivalent phase of the trial (whole square flashing) subtracted from them. To ensure there were sufficient trials in each condition, the attend top-left and attend bottom-left conditions were averaged to form an attend-left condition. Similarly, attend top-right and attend bottom-right were averaged to form an attend-right condition. There were therefore four conditions: pre-cue attend left, pre-cue attend right, retro-cue attend left, and retro-cue attend right.

Differences in mean amplitudes were assessed by repeated-measures ANOVAs, using the Greenhouse–Geisser epsilon correction for nonsphericity where appropriate (Jennings & Wood, 1976). Only the corrected probability values and degrees of freedom are reported. The ANOVA factors were side of attention (left, right), cue (pre-cue, retro-cue), hemisphere (left, right), and electrode (six sites). For the midline analysis, there were five electrode sites and no hemisphere factor. Effects of interest only included main effects or interactions involving side of attention and cue factors. Because of the risk of false-positive effects in the multiple interrelated comparisons in the regional analyses, results were only

considered significant if they persisted over at least two successive time bins in a given region (i.e., ≥ 80 msec).

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Note

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