BRIEF REPORTS

Implicit memory influences the allocation of attention in visual cortex

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The visual environment is highly regular, with particular objects frequently appearing in specific locations. Previous studies of visual search have shown that people take advantage of such regularities, detecting targets more quickly when they appear at a predictable location within a given spatial configuration. Moreover, this effect depends on implicit rather than explicit memory for the configurations. These studies have suggested that implicit long-term memory for contextual information influences the allocation of attention, modulating the flow of information through visual cortex. The present study used event-related potentials to provide the first direct support for this proposal. We suggest that this guidance of attention by implicit memory is important in the natural environment because it allows environmental regularities to influence perception without the intervention of limited-capacity conscious processes.

The human brain is a powerful parallel processing device, but many tasks require the use of *central* or *executive* processes that cannot easily operate in parallel (Logan & Gordon, 2001; Pashler, 1994a). The ability to engage in rapid, real-time sensorimotor interactions with the environment may depend on the ability to circumvent these central processes. For example, stimulus transients can attract attention automatically, leading to a change in the processing of sensory information without engaging central processes (Jonides, 1981; Yantis, 2000). This is a rather limited means of controlling sensory processing, however, because only a small fraction of task-relevant information is signaled by isolated stimulus transients. Similarly, extensive experience with a perceptual discrimination can lead to a more accurate representation of the discriminated stimuli in visual cortex (Gilbert, 1994). However, these perceptual learning effects require a very large number of exposures for a given discrimination and can be specific to the retinotopic locations in which these stimuli were presented.

Chun and Jiang (1998, 1999) described a more sophisticated form of unconscious control of sensory processing in which implicit associative memory for spatial context is used to guide the allocation of attention, presumably influencing the flow of sensory information. In these studies, subjects searched for a rotated T target presented among rotated L distractors (see Figure 1A), a search task that is known to require focused spatial attention (Wolfe, 1994). To examine implicit contextual learning, *novel arrays* consisting of randomly varying spatial configurations of items were randomly intermixed with a set of 12 *repeated arrays* that maintained their spatial configurations across trial blocks. Targets were always presented at a specific location within a given repeated array, such that the spatial structure of the array predicted the location of the target (but not its identity).

Reaction times (RTs) were reliably faster for targets appearing in repeated versus novel arrays after only five exposures to each of the repeating arrays, a benefit termed the *contextual cuing* effect. Additional tests have demonstrated that the contextual memories underlying this RT effect are implicit (Chun & Jiang, 2003), and subsequent investigations have demonstrated that they nonetheless rely on an intact hippocampal system (Chun & Phelps, 1999). Thus, hippocampally mediated implicit memory for spatial context can lead to improved visual search performance. More specifically, Chun and Jiang (1998, 1999) proposed that repeated exposure to a particular search array leads to the formation of an implicit memory that reflects learned associations between the location of the target and the surrounding visual context. When an incoming image matches one of these representations, the retrieved contextual memory guides attention to the target location, influencing the flow of information through visual cortex and allowing more rapid discrimination of the target. This hypothesis proposes that activation of implicit memories can lead to a top-down modulation of feed-forward perceptual processing in visual cortex. Although quite sensible, there is no precedent in the memory literature for the hypothesis that activation of an implicit memory can serve as a source of attentional control over the flow of information through visual cortex. If this could be shown, it would demonstrate a previously unknown role of implicit memory in controlling information processing.

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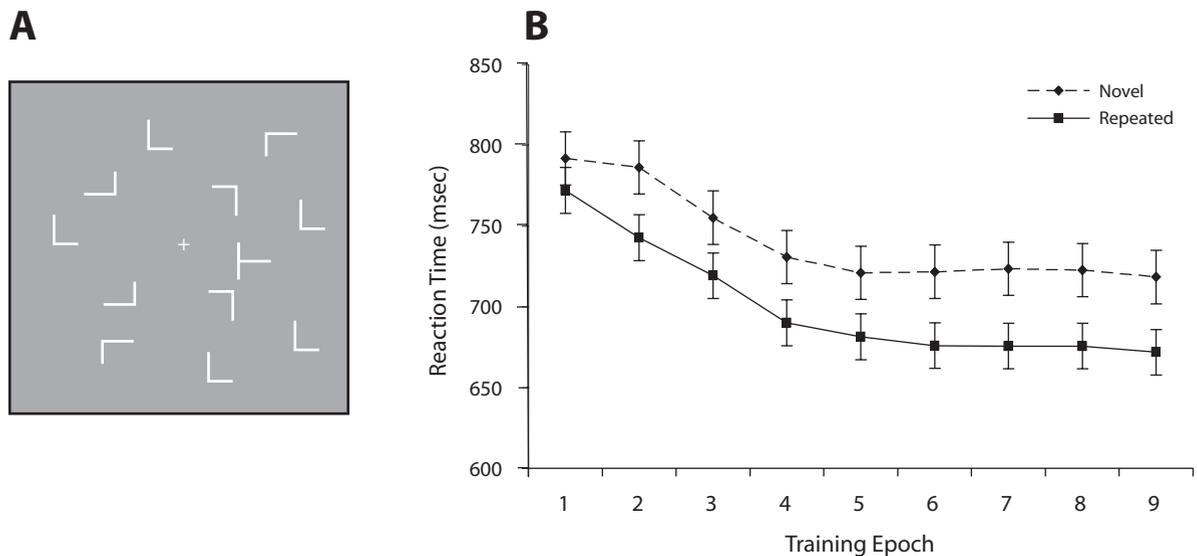
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Figure 1. (A) Example visual search array used in the present experiment and by Chun and Jiang (1998, 1999). Subjects are instructed to find the T in the display and indicate which direction it is facing. Contextual cuing is observed as a reduction in reaction time for repeated versus novel arrays. (B) Reaction time results from the present experiment, showing a reliable contextual cuing effect. Error bars reflect the standard error of the mean.

The phenomenon of contextual cuing demonstrates that implicit memory can influence the efficiency of visual search. However, the efficiency of search is influenced by postperceptual factors in addition to perceptual factors (Palmer, Ames, & Lindsey, 1993). For example, implicit memory could influence search by improving the efficiency of postperceptual decision processes, rather than by rapidly directing attention to the location of the target in repeating arrays as suggested by Chun and Jiang (1998, 1999). Because of this, behavioral methods alone (including eye movement recordings) are not sufficient to demonstrate that contextual cuing affects the flow of information through visual cortex. The goal of the present study, therefore, was to demonstrate that the contextual cuing effect actually reflects an influence of implicit memory on the allocation of covert attention within the visual system.

A previous study by Olson, Chun, and Allison (2001) examined whether implicit memory influences processing in visual cortex by recording intracranial event-related potentials (ERPs) from human subjects while they performed a contextual cuing task. Consistent with this possibility, they found that activity in striate and extrastriate visual areas reliably differentiated repeated from novel arrays following learning. However, there was no way to determine whether this reflected a reallocation of attention in visual cortex or simply a different response to familiar versus unfamiliar arrays. That is, these effects may have reflected the implicit memory itself rather than the focusing of attention onto the location of the search target.

To more specifically assess attentional modulations of perceptual processing in the contextual cuing paradigm, the present experiment focused on the scalp-recorded N2pc component, a well-validated electrophysiological signature of the focusing of attention (Luck, Girelli, McDermott, & Ford, 1997). This component is called *N2pc*

to reflect its typical timing (in the *N2* latency range), its scalp distribution (*p*osterior), and its lateralization (*c*ontralateral to the attended location). Multimodal imaging studies have shown that the N2pc component arises from ventral occipital regions within visual cortex (Hopf et al., 2006; Hopf et al., 2000). Moreover, the N2pc component appears to be a human ERP homologue of single-unit attention effects that have been observed in monkey visual cortex (Luck et al., 1997). Thus, the N2pc is well suited for investigating the contextual-cuing hypothesis.

Our central hypothesis is that contextual cuing increases the likelihood that one of the first few shifts of attention on a given trial will be to the target. This is the pattern that we would expect if observers search novel arrays in a random manner, occasionally finding the target right away, and if contextual cuing increases the probability that the target is found right away on repeated trials. If contextual cuing operates in this manner, we would expect to see a larger number of fast RTs for repeated than for novel arrays. It is not possible to measure single-trial N2pc latencies to see this pattern, but an increase in the probability of fast attention shifts would be expected to increase the amplitude of the early part of the averaged N2pc waveform, just as it would increase the early portion of the RT probability distribution. This is a consequence of the fact that an averaged ERP waveform reflects a convolution of the single-trial waveshape with the probability distribution of onset times (Luck, 2005).

Another possibility is that contextual cuing influences RT by allowing attention to be shifted to targets in repeated arrays faster than it is ever shifted to targets in novel arrays, rather than by increasing the likelihood of shifting attention directly to the target. However, distinguishing between these two alternatives is beyond the scope of the present work, and either possibility is consistent with the

hypothesis that implicit associative memory can influence the allocation of attention within visual cortex.

METHOD

Subjects

Twenty-one University of Iowa undergraduate volunteers participated in this experiment. Subjects received monetary payment ($8/h) for their participation. All reported having normal or corrected-to-normal vision.

Stimuli

The stimuli and task are illustrated in Figure 1A; they closely matched those used by Chun and Jiang (1998, 1999). The visual search items were white Ts and Ls presented within a 37.2º × 28.3º region centered at a continuously visible fixation point at the center of a gray screen at a viewing distance of 70 cm. The target was a T rotated 90º to the right or to the left, with equal probability. Nontarget stimuli were L-shaped objects in one of four possible orientations (0º, 90º, 180º, or 270º); the orientation of each was selected at random (with replacement). Each array contained a single target and 11 nontarget items. Each item subtended 2.3º × 2.3º, with a minimum center-to-center separation of 2º. Targets were additionally constrained to appear at least 1º to the left or right of the vertical meridian.

A set of 12 repeated arrays was generated at random for each subject. Novel arrays were generated at random for each novel trial. A randomly chosen target (either left or right facing) was generated on each trial. The target always appeared in the same location for a given repeated configuration, but its orientation was unpredictable. The distractor orientations remained constant across trials in repeated arrays.

To rule out location probability effects, target items were presented equally often in 24 out of the 36 possible target locations: We selected 12 of the locations for the repeated configurations and 12 for the novel configurations. Different sets of target locations were selected at random for each subject. With this design, differences in performance between repeated and novel arrays could not be due to absolute location likelihoods. The distractor locations for both novel and repeated trials were randomly sampled from all possible locations, including target locations used in other configurations.

Design and Procedure

Each search array was presented for 1,500 msec, followed by a blank intertrial interval of 300–800 msec. Subjects responded on each trial by using the right thumb to press one of two buttons to indicate whether the T pointed to the right or to the left. Speed and accuracy were equally emphasized.

Each session consisted of 54 experimental blocks of 24 trials (12 repeated arrays and 12 novel arrays presented in random order). The session began with a practice block of 144 trials, all of which used novel arrays. At the end of the session, subjects completed a recognition test. In this test, the 12 repeated arrays used in the experimental session and 12 new novel arrays were presented in random order, and subjects made an unspeeded buttonpress response to indicate whether they recognized the array.

ERP Recording

The electroencephalogram (EEG) was recorded from tin electrodes mounted in an elastic cap. The electrodes were placed at 10 sites from the international 10/20 system (F3, F4, C3, C4, P3, P4, O1, O2, T5, and T6) and at 2 nonstandard sites (OL, positioned halfway between O1 and T5, and OR, positioned halfway between O2 and T6). These sites and the right mastoid were recorded using a reference electrode at the left mastoid, and the ERP waveforms were algebraically rereferenced to the average of the left and right mastoids offline (Luck, 2005). The electrooculogram (EOG) was recorded between electrodes located lateral to the left and right eyes to monitor horizontal eye position, and an electrode beneath the left eye was used to monitor eye blinks. The EEG and EOG were amplified by an SA Instrumentation amplifier with a bandpass of 0.01–80 Hz and digitized at a rate of 250 Hz.

The N2pc component was isolated from the overall ERP waveform by creating difference waves in which the waveform for ipsilateral targets (left targets for left-hemisphere electrodes and right targets for right-hemisphere electrodes) was subtracted from the waveform for contralateral targets (left targets for right-hemisphere electrodes and right targets for left-hemisphere electrodes) and then averaging over the left and right hemispheres. N2pc amplitude was quantified from these difference waves at the P3/P4, O1/O2, OL/OR, and T5/T6 electrode sites as the mean voltage from 200 to 300 msec relative to a 200-msec prestimulus interval. N2pc onset latency was quantified as the time point at which the voltage reached 50% of the peak voltage. To increase the signal-to-noise ratio for the latency measures, the waveforms were first averaged across the P3/P4, O1/O2, OL/OR, and T5/T6 electrode sites.

For the ERP analyses, trials with blinks or clear eye movements were rejected prior to averaging using our standard procedures (Luck, 2005). The maximum allowable rejection rate was 25% of trials for a given subject; 3 subjects were replaced because they exceeded this criterion. The presence of small but systematic unrejected eye movements was assessed by creating averages for trials with a target on a given side of fixation. Residual eye movements in these averages were less than 0.65 μV in the direction of the target; this corresponds to an eye movement of approximately 0.04º of visual angle and to less than 0.02 μV of propagated electrical potential at the occipital electrodes.

RESULTS

Behavior

For the behavioral analyses, the data were grouped into nine epochs, each consisting of six blocks, with each block containing 12 novel arrays and one occurrence of each of the 12 repeated arrays. Figure 1B shows the mean RTs for repeated and novel arrays as a function of epoch. A repeated measures ANOVA with the factors epoch (1–9) and array type (repeated/ novel) revealed a significant main effect of epoch [$F(8,160) = 28.49, p = .0001$], reflecting the fact that RTs in both conditions decreased as subjects became more proficient at the search task throughout the course of the session. In addition, there was a main effect of array type [$F(1,20) = 20.83, p = .0001$], with significantly faster RTs for repeated arrays than for novel arrays, replicating the contextual-cuing effect. Some evidence of contextual cuing was found in all epochs, and the interaction between epoch and array type was not significant [$F(8,160) = 1.58$]. Paired t tests comparing repeated and novel RTs at each epoch revealed that the contextual-cuing effect was statistically significant beginning in the second epoch of trials [epoch 1, $t(20) = 1.715, p = .102$; all other epochs, $t(20) \geq 3.55, p < .002$]. Accuracy was above 95% correct for all conditions.

Figure 2A shows the probability distribution of RT for novel and repeated arrays, aggregated across all subjects. Short RTs (<700 msec) were more common for repeated arrays, and long RTs (>700 msec) were more common for novel arrays. These histograms reflect variance in RT across trials and subjects, and we therefore computed Vincentized cumulative RT distributions, which retain the shapes of the individual-subject distributions (Pashler, 1994b; Ratcliff, 1979). To compute these distributions, the RTs for a given subject in a given condition were divided into deciles, and the mean RT for each decile was then computed (see Fig-
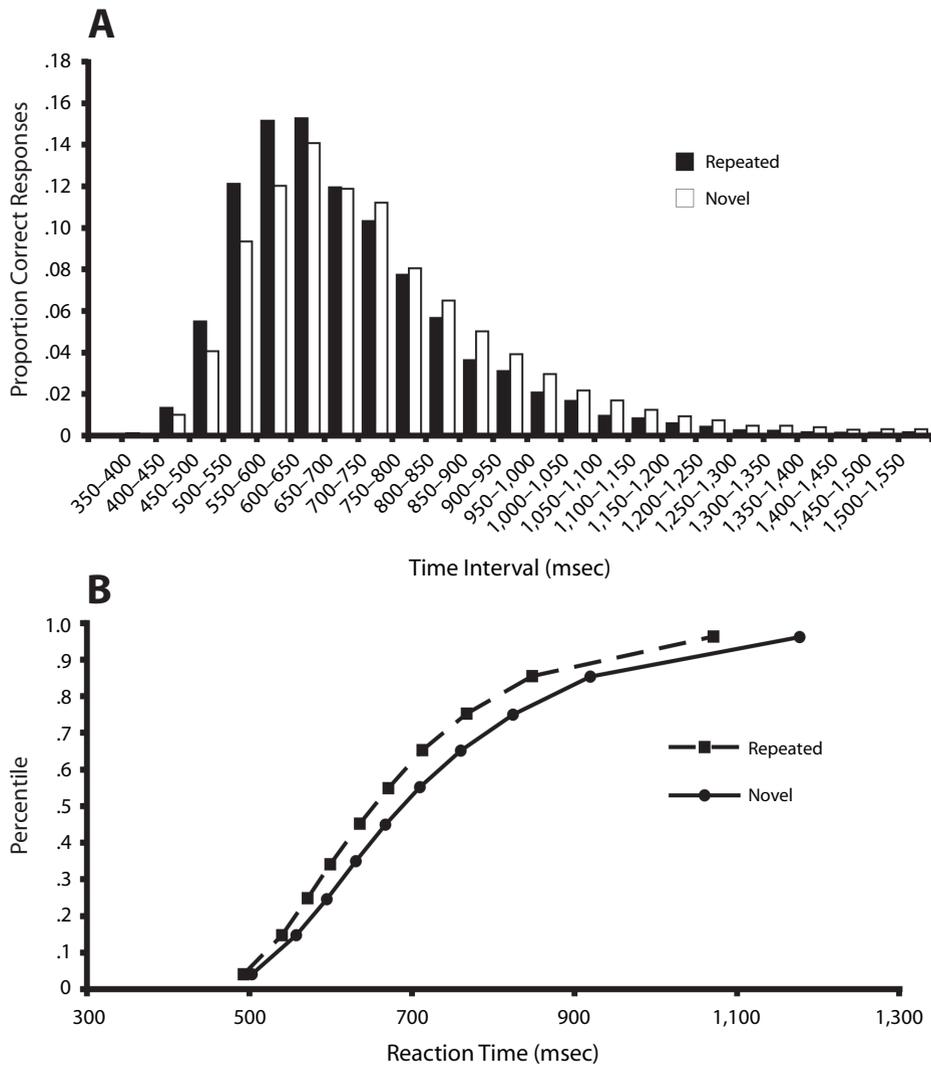
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Figure 2. (A) Probability distribution of reaction times, aggregated across all subjects, showing greater numbers of short-latency RTs (i.e., <700 msec) for repeated trials and greater numbers of longer-latency RTs (>700 msec) for novel trials. (B) Vincentized cumulative reaction time distributions for repeated and novel trials. Mean RT was faster for repeated trials across all deciles, although this difference only reached significance beginning with the second decile. Taken together, these data suggest that contextual cuing increases the likelihood of short-latency RTs.

ure 2B). The mean across subjects of these mean RTs is shown for each decile in Figure 2B. The difference in mean RT between novel and repeated arrays in the lowest decile was small (10 msec) and marginally significant [$t(20) =$ 2.01, $p = .058$]. In contrast, the difference at the second decile was larger (18 msec) and statistically significant [$t(20) = 3.48, p = .002$], and the difference remained significant in each subsequent decile (all $ps \leq .001$). Thus, these results are consistent with the proposal that contextual cuing increases the probability of fast RTs.[1]

In the recognition test given at the end of the session, subjects reported recognizing repeated arrays on 53% of trials and reported recognizing novel arrays on 51% of trials. This difference was small and not significant [$t(20) =$ 0.40, $p = .69$], which confirms that subjects had little or no explicit memory for the repeated arrays.

Electrophysiology

The N2pc component is defined as the difference in amplitude between the electrode sites contralateral and ipsilateral to the target item (Figure 3A), and it can be isolated from the rest of the ERP waveform by constructing contralateral-minus-ipsilateral difference waves (Figure 3B). Because contextual-cuing effects on RT were present beginning with the second epoch of trials, the ERP waveforms were averaged over Epochs 2–9. N2pc amplitude was greater for repeated arrays than for novel arrays beginning at approximately 175 msec, which is similar to the typical N2pc onset time for highly salient "pop-out" stimuli (Luck & Hillyard, 1994). Thus, this result indicates that memory for the repeated arrays allowed attention to be reliably shifted to the visual hemifield containing the target at relatively short latencies. Reliable but smaller
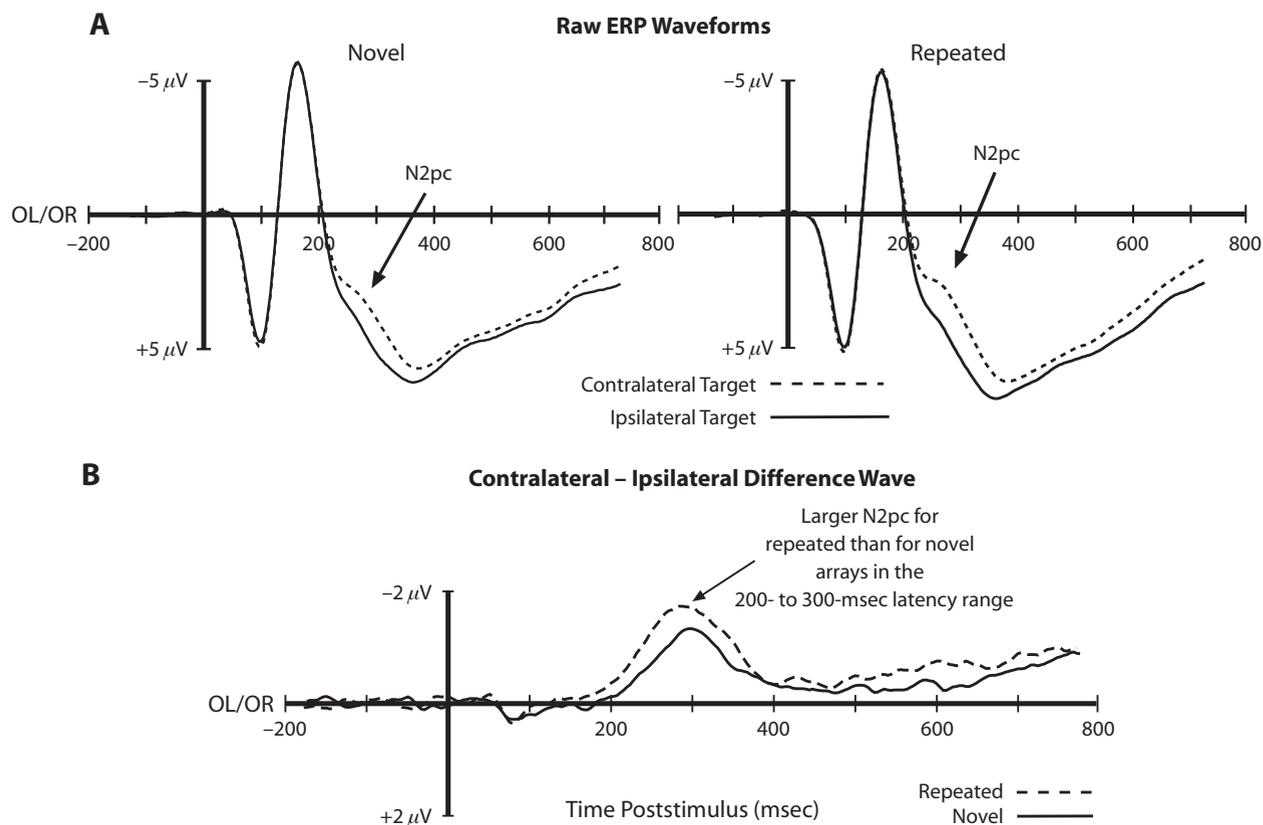
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Figure 3. (A) Grand-average ERP waveforms from occipitotemporal (OL/OR) electrode sites, averaged separately for contralateral and ipsilateral targets. The ERP waveforms shown here were low-pass filtered offline by convolving them with a Gaussian impulse response function with a full width at half maximum of 14.13 msec and a half-amplitude cutoff of approximately 30 Hz. (B) Contralateral minus ipsilateral difference waveforms, which isolate the N2pc component from the rest of the waveform. Negative is plotted upward.

N2pc activity was also observed during this time range for novel arrays, presumably because a random search occasionally leads attention immediately to the visual hemifield containing the target.

An ANOVA with the factors array type (repeated, novel) and electrode site (P3/P4, O1/O2, OL/OR, T5/T6) confirmed that mean N2pc amplitude from 200 to 300 msec was significantly greater for repeated arrays than for novel arrays [$F(1,20) = 4.92$, $p = .038$].[2] There was also a significant main effect of electrode site [$F(3,60) = 18.32$, $p < .0001$], reflecting the fact that mean N2pc amplitude was substantially larger at OL/OR and T5/T6 electrode sites than at P3/P4 and O1/O2. The array type × electrode site interaction was not significant ($p > .1$).

In an attempt to determine whether contextual cuing increased the overall speed of attention shifts, we also compared mean onset latency of the N2pc across conditions. Although the mean onset latency was 22 msec earlier for repeated arrays than for novel arrays, this difference was not significant [$t(20) = 0.30$, $p = .76$]. We measured and analyzed N2pc onset latency in many different ways, including using the jackknife method (Miller, Patterson, & Ulrich, 1998), but no approach yielded a significant difference. Although we cannot conclude from this that contextual cuing does not cause the fastest N2pc onset latencies to become even faster, the present data provide no convincing

support for this possibility. As stated previously, however, our main hypothesis—that contextual cuing modulates the flow of information through visual cortex—does not depend on whether contextual cuing influences the speed of the fastest RTs and the fastest shifts of attention.

DISCUSSION

The present study used ERPs to test the hypothesis that implicit long-term memory for contextual information influences the allocation of attention, modulating the flow of information through visual cortex. We obtained strong support for this hypothesis. We observed an increase in fast RTs for repeated arrays relative to novel arrays, accompanied by an increase in the amplitude of the early portion of the N2pc waveform. The increased N2pc amplitude from 200 to 300 msec poststimulus provides direct evidence that contextual cuing leads to greater early allocation of attention to the visual hemifield containing the target.

Taken together with the reaction time distributions depicted in Figure 2, this effect most likely reflects an increase in the probability that attention was directed to the target location as soon as preattentive processing made it possible to determine which configuration was presented. More specifically, N2pc amplitude from 200 to 300 msec was approximately 32% greater for repeated arrays than

for novel arrays, which suggests that contextual cuing increases the probability of an early attention shift by approximately 1/3.[3] Thus, contextual cuing does not guarantee that attention will shift immediately to the target location; it merely increases the probability that this will occur.

This interpretation is supported by eye movement data reported by Peterson and Kramer (2001), who found that contextual cuing increased the probability that one of the first few eye movements on a given trial landed on the target. Moreover, if a given eye movement did not land on the target, they observed no bias for it to land near the target, indicating that contextual guidance of attention is highly accurate on some trials and completely fails on other trials. Because eye movements are preceded by shifts of covert attention, these results suggest that the N2pc effects observed in the present study reflect shifts of attention directly to the target and not merely shifts of attention to the general region of the target.

These findings provide the first direct evidence that implicit long-term memory can modulate the processing of information in visual cortex on a trial-by-trial basis. The use of implicit memory to control attention may play a key role in real-time sensorimotor processing because it obviates the need to use prefrontal executive systems to guide an explicit memory search process, making perceptual processing faster and freeing executive systems to focus on other tasks. This idea complements previous research showing that attention can be focused on objects to discriminate them without storing them in visual working memory (Woodman, Vogel, & Luck, 2001) and without producing any awareness of the identities of the attended objects (Woodman & Luck, 2003a). Thus, visual attention may operate asynchronously from higher-level systems, with direct coordination occurring only when necessary.

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NOTES

1. It should be noted that the finding of somewhat faster RTs in the lowest decile is also consistent with the predictions of the increased-probability hypothesis. This hypothesis suggests that RTs are more likely to have been drawn from a "fast-RT" population distribution in the repeated condition than in the novel condition. As the number of RTs sampled from that distribution increases, so too will the speed of the fastest RTs. Because of this, it is impossible to differentiate between the increased-probability hypothesis and the speed-of-attention hypothesis of contextual cuing on the basis of the RT distribution analysis reported here.

2. In addition, we also compared mean amplitude for repeated versus novel arrays in the time range of the P1 ERP component (i.e., 75–125 msec poststimulus). Differences in the P1 time range could reflect imbalances in the visual display that could be contributing to the lateralization in the N2pc time range. This analysis produced no significant main effects or interactions (all $ps > .12$).

3. This assumes that attention—and the N2pc component—was either present or absent from the target hemifield during this time period, in which case N2pc amplitude in the averaged waveform would be proportional to the probability that the N2pc component was present. This assumption is consistent with previous evidence showing that the N2pc component reflects a strictly serial process under similar conditions (Woodman & Luck, 2003b).