Inhibition of Return in the Covert Deployment of Attention: Evidence from Human Electrophysiology

John J. McDonald, Clayton Hickey, Jessica J. Green, and Jennifer C. Whitman

Abstract

■ People are slow to react to objects that appear at recently attended locations. This delay—known as inhibition of return (IOR)—is believed to aid search of the visual environment by discouraging inspection of recently inspected objects. However, after two decades of research, there is no evidence that IOR reflects an inhibition in the covert deployment of attention. Here, observers participated in a modified visual-search task that enabled us to measure IOR and an ERP component called the posterior contralateral N2 (N2pc) that reflects the covert deployment of attention. The N2pc was smaller when a target appeared at a recently attended location than when it appeared at a recently unattended location. This reduction was due to modulation of neural processing in the visual cortex and the right parietal lobe. Importantly, there was no evidence for a delay in the N2pc. We conclude that in our task, the inhibitory processes underlying IOR reduce the probability of shifting attention to recently attended locations but do not delay the covert deployment of attention itself. ■

INTRODUCTION

When searching cluttered visual scenes, observers often must attend to objects one by one to find objects of interest (Woodman & Luck, 1999). This type of visual search is believed to involve an inhibition of recently attended locations that reduces the likelihood of inspecting the same locations repeatedly (Najemnik & Geisler, 2005; Klein, 1988). Evidence for such inhibition comes from laboratory tasks in which participants respond to targets that are preceded by salient but spatially nonpredictive peripheral stimuli. Under many conditions, participants respond more slowly to targets that appear at recently stimulated locations than to targets that appear elsewhere in the display (Klein, 2000; Maylor & Hockey, 1985; Posner & Cohen, 1984). This effect has been labeled inhibition of return (IOR; Posner, Rafal, Choate, & Vaughan, 1985).

The hypothesis that IOR reflects a mechanism responsible for guiding exploration of the visual environment has received support from behavioral studies of visual search. These studies have shown that when people move their eyes around a cluttered visual display in search of a target item, they are slower to respond to probes that appear suddenly at previously searched (distractor) locations than at novel (empty) locations (Müller & von Mühlenen, 2000; Klein & MacInnes, 1999; Klein, 1988). The increased probe detection times have been taken as evidence for inhibitory biasing of search, but because participants made eye movements in each of these studies, it is unknown whether the inhibitory bias affects the covert deployment of attention or some other nonattentional process. A similar longstanding debate centers on the nature of the inhibitory effects observed in more typical paradigms used to study IOR, such as the cue–target and target–target paradigms. Some investigators have proposed that IOR reflects inhibition of motor processes (Taylor & Klein, 2000; Posner et al., 1985), whereas other investigators have proposed that IOR reflects the inhibition of perceptual processes (Spalek & Di Lollo, 2007; Handy, Jha, & Mangun, 1999) or the covert deployment of attention (Reuter-Lorenz, Jha, & Rosenquist, 1996).

After decades of research, there is still no evidence for a bias or delay in the covert deployment of attention in visual-search or IOR tasks. This debate has not been resolved for several reasons. First, in the context of visual search, no one has sought to determine whether shifts of attention to previously inspected items are delayed or less likely when search is performed without eye movements. Second, the behavioral measures used thus far to study IOR and IOR-related deficits (e.g., reduced perceptual sensitivity; Handy et al., 1999) do not isolate attentional processes, thereby making it impossible to determine whether IOR arises due to a change in attention. Third, IOR is typically identified by comparing performance across conditions that differ in terms of basic sensory stimulation (i.e., recently stimulated vs. unstimulated). Such deficits could be the result of sensory refractoriness: The appearance of an initial

Simon Fraser University, British Columbia, Canada

stimulus could cause neurons to be in an unresponsive, refractory state upon the arrival of a second, task-relevant stimulus regardless of where attention is focused. In light of these problems, prior studies have not demonstrated that IOR is tied to attention (Berlucchi, 2006).

ERPs and other EEG measures have been used in a growing number of studies to investigate whether IOR affects relatively early or late processes (Pastötter, Hanslmayr, & Bäuml, 2008; Prime & Ward, 2004, 2006; Wascher & Tipper, 2004; McDonald, Ward, & Kiehl, 1999). In most of these studies, peripheral visual cues modulated subsequent target-evoked activity in the first 100–200 msec after target onset. When the cue–target SOA was appropriate for measuring IOR (>300 msec), targets elicited *smaller* P1 and/or N1 components over the posterior scalp when they were presented at cued locations than when they were presented at uncued locations (Prime & Ward, 2004, 2006; McDonald et al., 1999). These results provide converging evidence that peripheral cueing can impair sensory and perceptual processing of subsequent target stimuli presented at nearby locations. However, it is unknown whether the P1/N1 reductions arise from an inhibition of the covert deployment of attention or some other process because the P1 and the N1 are affected by sensory as well as attentional processes. Thus, it is possible that peripheral cues lead to reduced P1/N1 components because neurons that respond to both cue and target are in a state of refractoriness by the time the target appears. This sensory-refractoriness explanation has been considered in prior ERP studies of IOR (e.g., McDonald et al., 1999; see also Prime & Ward, 2006), but it has not been ruled out.

Here, we investigated whether IOR reflects a change in covert attention by examining a component of the visual ERP that is known to reflect the deployment of attention in visual space. This component, which begins approximately 175 msec after the onset of a multi-item display (Luck & Hillyard, 1994), is apparent as a greater negativity in the ERP waveform recorded over posterior scalp contralateral to the attended item than ipsilateral to the attended item. This difference—known as the posterior contralateral N2 (N2pc)—reflects attentional modulation of neural activity in visual cortex contralateral to the attended item (Hopf et al., 2000; Luck & Ford, 1998; Luck, Girelli, McDermott, & Ford, 1997) and can be used to track rapid shifts of attention in space (Hickey, McDonald, & Theeuwes, 2006; Woodman & Luck, 1999). We reasoned that if IOR modulates the N2pc, then logically, IOR would reflect a change in covert attention.

We recorded electrical brain activity from neurologically healthy individuals while they participated in a novel task that combined elements of standard target–target tasks used to study IOR (successive targets, reorienting events at fixation) with elements of standard visual-search tasks (multiple-element arrays). Participants viewed sequences of stimulus displays that each might contain a target item. To avoid the problem of sensory refractoriness, target stimuli were presented concurrently with nontarget stimuli on the opposite side of fixation, such that over successive trials, a target would appear at the location of a preceding target or at the location of a preceding nontarget of equal luminance (Figure 1). This enabled us to compare neural responses to targets presented at recently attended locations (repeat condition) and recently unattended locations (change condition) without having a large difference in sensory stimulation between the two conditions. We also compared neural responses in the repeat and the change conditions to responses in a neutral condition, in which a target display followed a nontarget display. This was done to determine whether target processing was inhibited at the previously attended location, facilitated at the previously unattended location (Pratt, Spalek, & Bradshaw, 1999), or both.

The main goal of the present study was to determine whether attention is inhibited from returning to recently attended locations. Restated in terms of IOR, the main goal was to determine whether IOR reflects at least in part an inhibition of the covert deployment of attention. If IOR is not associated with any modulation of attention (inhibition or otherwise; the nonattentional hypothesis), the timing and amplitude of the N2pc would be similar in the repeat, the neutral, and the change conditions. In contrast, if IOR is associated with a modulation of

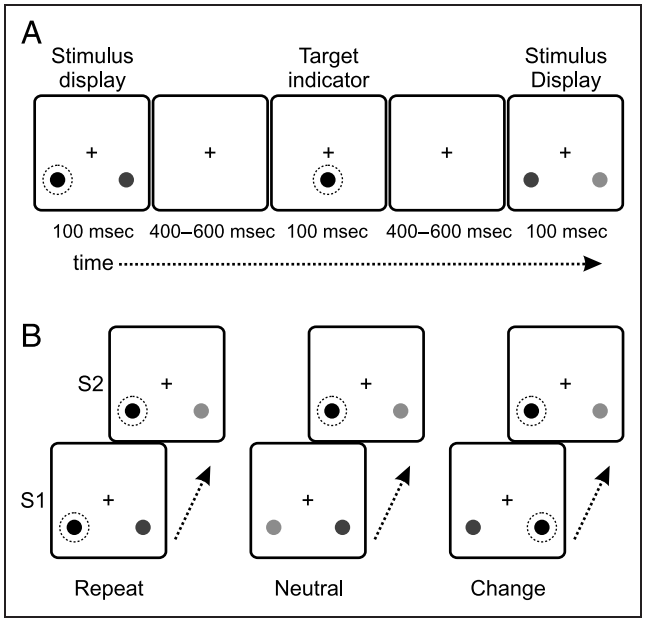

Figure 1. Illustration of stimulus sequences with target circle highlighted by a dashed ring. (A) Example of successive stimulus displays separated by target indicators and fixation displays. (B) Successive stimulus displays S1 and S2 in repeat, neutral, and change conditions. Intervening target indicators and fixation displays are not shown.

attention, the characteristics of the N2pc would vary across conditions.

Because of the sensitivity of our electrophysiological measure, we were able to test predictions from two different attentional accounts of IOR. If IOR reflects a delay in the reorientation of attention to recently attended locations (the delayed-attention hypothesis), the N2pc would occur later in the repeat condition than in the neutral and the change conditions. Alternatively, if IOR reflects a reduced likelihood of returning attention to previously attended locations (the biased-attention hypothesis), the N2pc would be smaller in the repeat condition than in the neutral condition. In this case, instead of simply being slow to shift attention to repeat-location targets, participants would actually shift attention to the nontarget on some trials. Crucially, the N2pc activity elicited on these trials would counteract the N2pc activity elicited when attention was shifted to the target in the opposite visual field, thereby reducing the overall N2pc amplitude when averaged across all repeat trials.

METHODS

Participants

Seventeen neurologically typical university students (mean age ± SD = 24.1 ± 4.3 years; 7 women; 15 right-handed) participated in the experiment after providing informed written consent. Each participant reported normal or corrected-to-normal visual acuity and normal color vision.

Stimuli and Procedure

Each participant viewed 1,080 stimulus displays that each consisted of two colored discs presented 4° below and 6° to the left and right of fixation. The discs were selected randomly from three colors (green, cyan, and magenta) such that no stimulus display contained two like colors. Two thirds of the stimulus displays contained a target disc and a nontarget disc, and the remaining stimulus displays contained two nontargets. Target and nontarget stimulus displays were randomly intermixed, and each one was preceded by a target-indicator display that contained a colored disc presented 4° below fixation. The target indicator served to identify which of the three discs was the target and also to reorient attention to a nonlateralized location between successive stimulus displays. The color of the target indicator remained constant throughout the experiment and was counterbalanced across participants. The timing of each event is shown in Figure 1A. Participants were required to indicate whether the target, if present, was located on the left or right by pressing one of two buttons as quickly as possible and to refrain from responding if the display contained two nontargets. Participants pressed a left button for left targets and a right button for right targets. The hand used for responding was counterbalanced across participants. All procedures were approved by the Simon Fraser University research ethics board.

Behavioral Analysis

We measured IOR behaviorally as a function of the locations of successive targets (Maylor & Hockey, 1985). The second of two successive stimulus displays, denoted S2, was categorized as belonging to the repeat, the change, or the neutral condition if the preceding stimulus display, denoted S1, contained a target on the same side, a target on the opposite side, or two nontargets, respectively (Figure 1B). The median RT to targets on S2 displays was computed for each condition for each participant, and this value was averaged across participants. To determine whether IOR occurred, we subtracted the mean RT in the repeat condition from the mean RT in the change condition (change RT minus repeat RT). A negative RT difference indicated the presence of IOR. We further compared the mean RT observed in the repeat and change conditions to the mean RT observed in the neutral condition. This allowed us to determine whether responses to targets presented at previously attended locations were delayed (neutral RT minus repeat RT) and whether responses to targets presented at previously unattended locations were facilitated (Pratt et al., 1999) (neutral RT minus change RT). Finally, we investigated the duration of IOR by examining separately the mean RTs to the first repeated target (e.g., S1 nontarget, S2 left, S3 left) and the second repeated target (e.g., S1 left, S2 left, S3 left).

Electrophysiological Recording and Analysis

We recorded the EEG from 63 electrodes. Signals were amplified with a gain of 20,000 and a passband of 0.1–100 Hz, digitized at 500 Hz, and averaged off-line. The resulting ERPs were then low-pass filtered by convolving them with a Gaussian impulse response function with a standard deviation of 4 msec and a half-amplitude cutoff at approximately 45 Hz. Events that were contaminated by eye blinks, horizontal eye movements, or amplifier blocking were excluded from ERP averaging. Lateralized ERP waveforms were computed by collapsing over left and right stimulus locations and left and right recording hemispheres. For example, ERPs contralateral to the target were computed by averaging the ERPs recorded over the right scalp when the target was on the left with the ERPs recorded over the left scalp when the target was on the right. For target displays, the amplitude of the N2pc was quantified as the mean voltage within a 175- to 225-msec poststimulus latency window, relative to a 100-msec prestimulus baseline period. For nontarget displays, the N2pc was measured in a slightly later time window (225–275 msec) centered on the peak negativity. The

latency of the N2pc was measured based on ipsilateral-minus-contralateral difference waves using a measure of fractional area with a 50% criterion. The N2pc area was measured across a 100- to 300-msec latency period. Differences in N2pc latency between conditions were statistically assessed using a jackknife procedure (for details, see Kiesel, Miller, Jolicoeur, & Brisson, 2008). Latency analysis was conducted on data prior to off-line digital filtering.

Differences in RTs, N2pc peak latencies, and N2pc amplitudes were tested in separate within-subject analyses of variance with factors for Target location (left and right) and Condition (repeat, neutral, and change). The significance level was set at .05 for each test. Planned pairwise comparisons were two-tailed and Bonferroni adjusted to maintain family-wise error rates at .05.

Neural Source Estimation

The cortical generators of the N2pc waves were based on the left-target minus right-target difference waves. Discrete estimates of the current sources of N2pc were estimated using BESA 5.1. A single pair of dipoles was fit to the ERP difference wave in the 175- to 225-msec time interval. The dipole pair was constrained to be symmetric in location only. The coordinates of each dipole were registered on a standardized finite element model that was created from an averaged head using 27 individual MRIs in Talairach space.

Beamformer source estimates for each participant were computed separately for the repeat and the change conditions using BESA 5.1. The BESA multiple source beamformer is a linearly constrained minimum variance beamformer, which estimates activity in the brain voxel by voxel using the cross-spectral density matrix (Gross et al., 2001; Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997). The beamformer acts as a spatial filter that estimates the contribution of activity at one point in the brain while minimizing interference from other sources in the brain. After computing the beamformer sources for individual participants in BESA, differences between repeat and change conditions were assessed statistically by random permutation tests in fMRI software (Cox & Hyde, 1997). Significant sources were then displayed on the same average brain used in the dipole analysis.

RESULTS

Figure 2 shows the ERP waveforms elicited by the second of two consecutive target displays (S2) in the repeat, the neutral, and the change conditions. Each waveform consisted of a series of positive and negative peaks, including the P1 (mean latency of 114 msec), N1 (164 msec), P2 (214 msec), and N2 (254 msec) components (Figure 2A). The timing and amplitudes of the early P1 and N1 components, which reflect early evoked

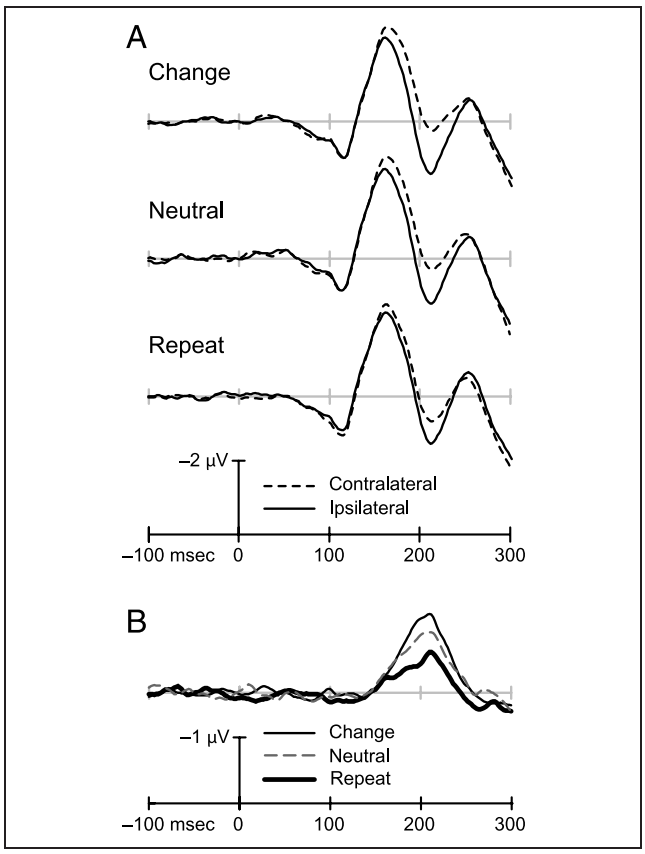

Figure 2. Grand averaged ERP waveforms time-locked to S2 in repeat, neutral, and change conditions, recorded at lateral occipital electrode sites (PO7, PO8). The time scales are referenced to the onset of S2 at 0 msec. Negative voltage is plotted upward. (A) ERPs recorded contralateral and ipsilateral to the target side, collapsed over left-target and right-target displays. (B) ERP difference waves created by subtracting the ipsilateral-to-target waveform from the contralateral-to-target waveform.

activity in extrastriate visual cortex, did not vary as a function of condition, Fs < 1. These null effects indicate that directing attention to a target on one display did not affect low-level sensory and perceptual processing of stimuli on the subsequent display. The present experiment had the advantage of eliminating sensory differences between conditions, which suggests that P1 and N1 modulations found using standard cue–target and target–target paradigms are due to sensory-driven processes such as sensory refractoriness. This conclusion is bolstered by the fact that peripheral cueing leads to a reduced target-elicited P1 component whether or not IOR is observed behaviorally (Wascher & Tipper, 2004).

Beginning approximately 175 msec after the onset of S2, the posterior ERP waveforms recorded contralateral to the target were more negative than the posterior ERP waveforms recorded ipsilateral to the target (Figure 2A). These contralateral–ipsilateral differences indicate that the N2pc was present to a greater or lesser degree in each of the three conditions. To examine the N2pc more closely, we subtracted ERPs recorded ipsilateral to the

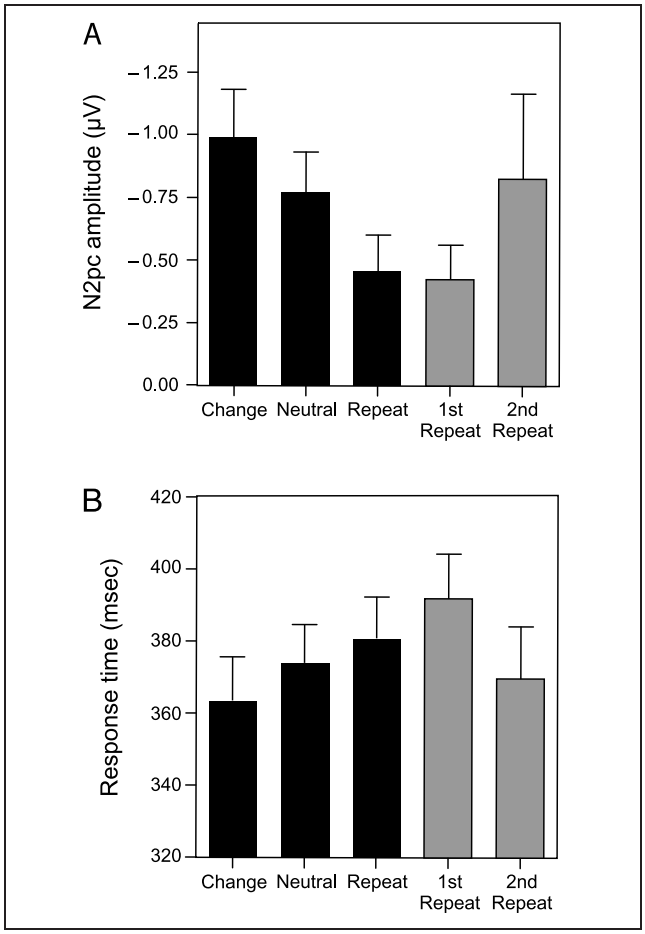

Figure 3. Mean response times and N2pc amplitudes for S2 target displays. Black bars show results from repeat, neutral, and change conditions, and gray bars show results from the first and second repeated target displays separately. Standard error bars are shown. (A) N2pc amplitudes. (B) Response times.

target from corresponding ERPs recorded contralateral to the target and plotted the resulting difference waveforms (Figure 2B). The N2pc can be seen in each of these difference waveforms as a negative voltage that peaks at approximately 210 msec poststimulus. Visual inspection of the difference waveforms suggests that the N2pc began and peaked at the same times across all three conditions and ended earlier in the repeat condition than in the other conditions. N2pc latencies were assessed using a jackknife approach applied to fractional area measures with a 50% criterion (see Kiesel et al., 2008). This analysis was conducted on data prior to offline digital filtering. N2pc latency was unaffected by condition, $F(2,32) < 1$. In contrast, the amplitude of the N2pc did vary across conditions, $F(2,32) = 9.52$, $p = .001$. The N2pc was smallest in the repeat condition, intermediate in the neutral condition, and largest in the change condition (−0.46, −0.77, and −0.99 μV, respectively; Figure 3A). As predicted based on the biased-attention hypothesis, the N2pc was smaller in the repeat condition than in either of the neutral or the change conditions, $p = .02$ and $p = .004$. The N2pc waves in the neutral and the change conditions were not statistically different, $p = .32$.

To confirm that the behavioral IOR effect occurred in the present experiment, we compared response times (RTs) to S2 targets in the repeat, the neutral, and the change conditions. RTs were longest in the repeat condition, intermediate in the neutral condition, and shortest in the change condition, $F(2,32) = 5.84$, $p = .013$ (383, 375, and 364 msec, respectively; Figure 3B). The 18-msec difference between repeat and change conditions was statistically significant, $p = .001$, which suggests that IOR did occur in the present experiment. Neither the mean RT in the repeat condition nor the mean RT in the change condition differed significantly from the mean RT in the neutral condition (ps $> .38$).

To determine how long the inhibitory effects lasted, we analyzed the data as a function of the number of successive targets presented at the same location. Figure 3 shows the N2pc amplitudes and mean RTs for target displays preceded by just one same-location target display (first repeat) or two same-location target displays (second repeat). Consistent with previous findings (Maylor & Hockey, 1987), the magnitude of IOR decreased over successive repetitions of same-location targets. Specifically, we found behavioral inhibition for the first repeated target, $p = .02$, but not for the second repeated target, $p = .58$ (Figure 3B, gray bars). The same pattern was found for N2pc amplitudes: The N2pc was reduced for the first repeated target, $p = .003$, but not for the second repeated target, $p = .35$ (Figure 3A, gray bars).

To further investigate the hypothesis that attention was biased against returning to the location of the previous target, we separately examined the N2pc elicited in the fastest and slowest repeat trials (Figure 4). According to the biased-attention hypothesis, attention would have shifted initially to the location of the nontarget, rather than the target, on some of the repeat trials. Such a shift of attention would lead to increased RT and smaller N2pc waveforms across trials. Repeat trials were divided into fast repeats and slow repeats based on a median

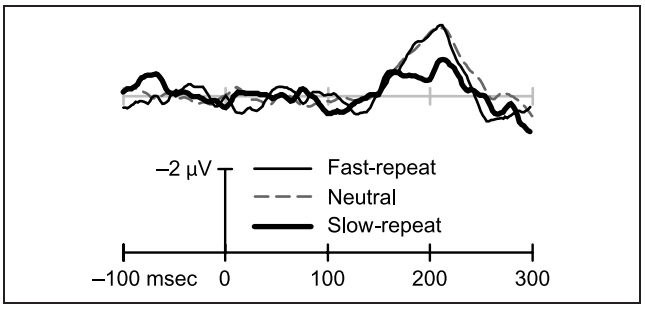

Figure 4. ERP difference waves created by subtracting the ipsilateral-to-target waveform from the contralateral-to-target waveform for each of the fast-repeat, slow-repeat, and neutral conditions.

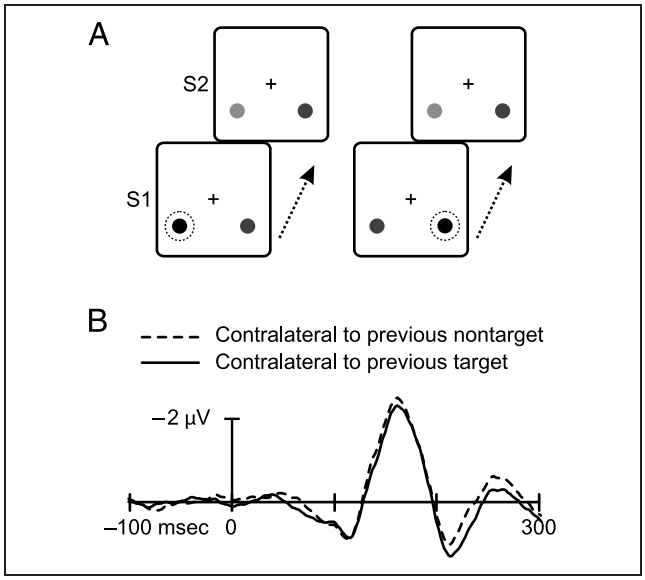

Figure 5. ERP waveforms to nontarget displays following target displays. (A) Illustration of a nontarget display (S2) preceded by a stimulus display (S1) containing a target on the left or right side (highlighted by dashed ring). The nontarget display always consisted of two different nontargets, here denoted as different shades of gray. (B) Grand averaged ERP waveforms time-locked to the S2 nontarget display, recorded at lateral occipital electrode sites (PO7, PO8) contralateral to the target and nontarget on the preceding S1 display.

split of the RTs. Mean RT in fast repeats was 331 msec (SD = 39), whereas mean RT in slow repeats was 441 msec (SD = 55). The N2pc for the fast-repeat trials was significantly larger than the N2pc for the slow-repeat trials, p = .02, and was not significantly different from the N2pc observed in the neutral condition, p = .68. The N2pc for the slow-repeat trials was not significantly different from zero, p = .29.

Finally, we measured the ERPs elicited by nontarget displays to determine whether an attentional bias would be found when stimuli require no manual response. On the basis of our N2pc results, thus far, we predicted that nontarget displays would elicit an N2pc contralateral to the location of the unattended stimulus on the preceding target display (i.e., away from the location of the preceding attended stimulus; Figure 5A). This is indeed what we found: ERPs recorded over the posterior scalp were more negative contralateral to the preceding nontarget than contralateral to the preceding target, p = .0001 (Figure 5B).

To estimate the neural sources of the N2pc amplitude effects, we first created spherical spline-interpolated voltage maps of ERP activity in the N2pc time range separately in the repeat and the change conditions (Figure 6A). Difference waves were constructed by subtracting the right-target ERP waveforms from the left-target ERP waveforms in each condition. Such difference waves isolate lateralized cognitive activity that is primarily related to the N2pc in the 200- to 250-msec interval (Hopf et al., 2000). Each difference map shows negative voltage over

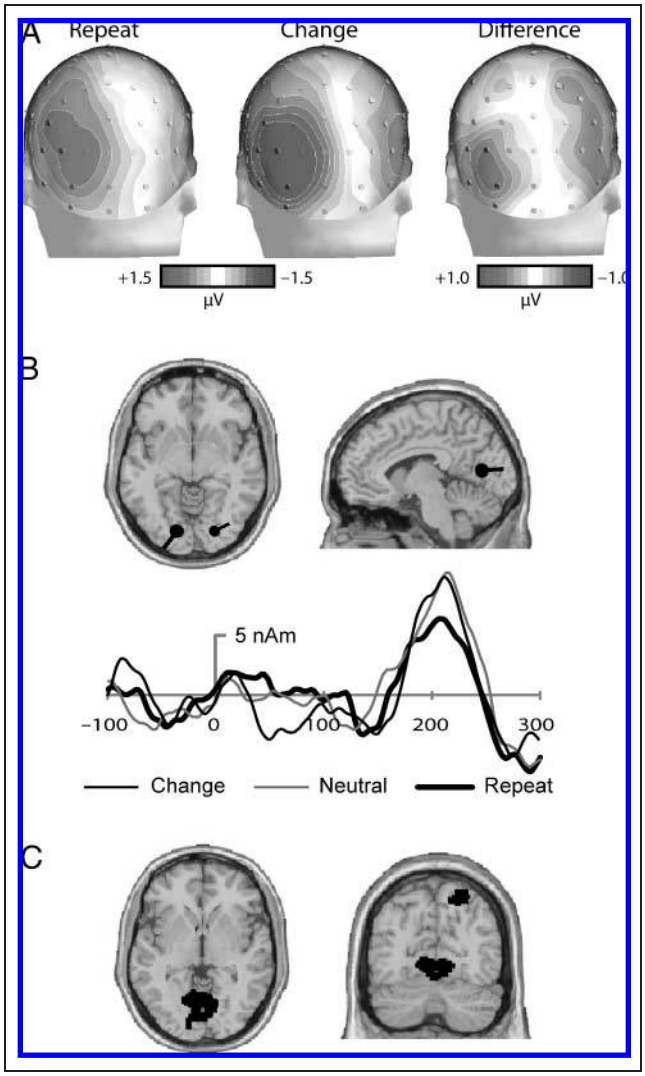

Figure 6. Scalp topographies and estimated neural sources of the N2pc activity. (A) Scalp topographies of the grand-average N2pc waveforms (175–225 msec) plotted on a standarized boundary element head model. The leftmost and the center maps show N2pc scalp topographies based on the left-target minus right-target difference waves in the repeat and the change conditions, respectively. The rightmost map shows the scalp topography of the difference waveform obtained by subtracting the N2pc activity in the repeat condition from the N2pc activity in the change condition. All maps show a negative ERP peak over the right posterior scalp and a positive ERP peak over the left posterior scalp. (B) Dipoles plotted on standard MRIs and corresponding source waveforms. A symmetric pair of dipoles (x = ±20, y = −75, z = −4) were fit over the 175- to 225-msec interval for the neutral condition, then the same source model was applied to the change and repeat data. The source waveforms are shown only for the dipole in the left hemisphere as the pattern of results was the same for the right hemisphere dipole. (C) Beamformer sources of the difference in alpha-band (8–12 Hz) activity between the change and the repeat conditions during the N2pc time range. Bilateral sources were observed in the lingual gyrus (x = ±6, y = −69, z = −2) as well as a source in the right parietal cortex (x = 20, y = −77, z = 54).

the right occipito-temporal scalp and a more focal positive voltage over the left occipito-temporal scalp; the positivity appears because the subtraction inverted the sign of the contralateral negativity that was elicited when

the target was on the right. The difference between the N2pc voltages in the repeat and the change conditions had a similar scalp distribution, with foci located over the lateral occipital scalp (Figure 6A, right). The scalp topography of this latter difference suggests that IOR is associated with modulations of neural activity in visual regions of cortex.

The neural generators of the N2pc activities were modeled as dipole current sources fit to the left–right difference topographies in the change, the neutral, and the repeat conditions. A single pair of symmetric dipoles accounted for the posterior scalp activity over a 50-msec time interval that was centered on the N2pc peak latency (175–225 msec). The residual variances for the repeat, the neutral, and the change conditions were 10.0%, 7.1%, and 8.4%, respectively. The best-fitting dipoles were projected onto a standardized brain and localized to the lingual gyrus of the occipital cortex (Talairach coordinates: $x = \pm 20, y = -75, z = -4$; Figure 6B). As shown in Figure 6B, the source waveforms showed the same pattern as the scalp-recorded N2pc waves; specifically, the timing of the occipital source activity was similar across conditions, but the amplitude of the source activity was reduced in the repeat condition. These findings demonstrate that IOR is associated with modulations of neural activity in extrastriate visual cortex.

The scalp topography of the change-repeat difference shown in Figure 5 (right) suggested that IOR was associated with modulation of activity in parietal as well as occipital brain areas. Rather than attempting to model this IOR-related difference topography with discrete dipoles, we opted to use the multiple source beamformer analysis in BESA, which does not require a priori specification of the number of sources contributing to the scalp-recorded activity. Our beamformer analysis focussed on alpha-band (8–12 Hz) activity in the N2pc time range because an initial time-frequency analysis found that the difference between repeat and change conditions in the latency of the N2pc was within this frequency band. Figure 6C shows the resulting beamformer sources of the IOR-related decrease in N2pc. Consistent with our dipole source analysis, one source of activity was found to be in the region of the lingual gyrus ($x = \pm 6, y = -69, z = -2$). A second source was found to be in the right posterior parietal cortex (BA 7; $x = 20, y = -77, z = 54$).

DISCUSSION

Across a variety of fields, IOR is widely accepted to be a mechanism that guides visual exploration by discouraging the re-inspection of objects. As a result of this mechanism, observers are biased to move their eyes to locations of new objects. Although it is clear that IOR helps guide oculomotor search, there has been no evidence to date to suggest that IOR is associated with a change in the covert deployment of attention. In the present study, we used the N2pc to determine if IOR reflects a modulation in covert attention. The timing of the N2pc was unaffected by the location of prior attentional deployment, but the amplitude of the N2pc was reduced for targets that appeared at recently attended locations relative to targets appearing at unattended locations and neutral locations. The N2pc amplitude reduction provides the most decisive evidence to date that IOR is an attentional phenomenon.

The overall pattern of N2pc activity—reduction in amplitude with no change in latency—is inconsistent with the view that people are simply slow to orient attention back to recently attended locations. Instead, this pattern demonstrates that people are probabilistically biased to orient attention away from recently attended locations, at least under the conditions studied here. These results are inconsistent with conclusions drawn from one of the seminal articles on IOR. In the very study in which Posner et al. (1985) coined the term ''inhibition of return'' to signify its presumed role in guiding visual search, it was concluded that IOR reflects an inhibitory bias in the overt movement of the eyes but not in the covert deployment of attention. The N2pc amplitude data observed here show that inhibitory biases help to guide covert, as well as overt, inspection of the visual environment.

Consistent with previous research (Maylor & Hockey, 1987), we found that behavioral IOR lasted for a single target repetition. By the second repetition of a target location, the speed of manual responses returned to baseline levels. Importantly, the ERP data mirrored this behavioral pattern, with N2pc amplitude returning to the neutral baseline level for the second repetition of a target location. In addition, the N2pc was smallest when responses on repeat trials were slowest. Together, these results suggest a close relationship between N2pc modulation and behavioral IOR.

Converging electrophysiological evidence for an attentional bias was obtained when the target stimulus was absent and observers made no manual response. Under these circumstances, the N2pc was observed contralateral to the location that was *unattended* on the immediately preceding trial. In other words, people oriented their attention away from the recently attended location even when no target appeared on the current trial, and therefore no overt response was necessary.

The sources of IOR-related N2pc activity were localized to the lingual gyri of the occipital lobes and the right parietal cortex. These findings are consistent with prior source analyses of the N2pc and current theories of attention. A prior MEG study revealed that the N2pc arises from neural sources in parietal and occipitotemporal cortices (Hopf et al., 2000). The parietal-lobe source was hypothesized to reflect the actual deployment of attention in space, whereas the occipital-lobe source was hypothesized to reflect the attentional selection of the target stimulus. In light of this, the current findings

indicate that IOR reflects a bias in attention-shift processes in the parietal lobe as well as modulation of attention-related processes in the occipital lobe.

Because the goal of the present study was to isolate a possible attentional effect associated with IOR, it is not possible to rule out the possibility that IOR can arise from modulations of nonattentional processes. In fact, it is quite likely that IOR can arise from changes in many different processes. Converging lines of evidence point to a sensory component to IOR in cue–target and target–target paradigms. For example, IOR can be found at the locations of two simultaneous peripheral cues when the cue–target SOA is relatively short SOA (Tassinari & Berlucchi, 1993; Posner & Cohen, 1984). Moreover, peripheral cues lead to reduction of the P1 ERP component even when no IOR is present, which suggests that peripheral cuing may lead to sensory refractoriness, which might in turn contribute to IOR (Wascher & Tipper, 2004; McDonald et al., 1999). Other recent evidence point to inhibition of response processes in cue–target and target–target tasks. In particular, IOR has been associated with increased synchrony in beta-band EEG oscillations that presumably originate in motor cortex (Pastötter et al., 2008).

The present study also does not rule out the possibility that IOR is associated with a delay in covert deployment of attention or a facilitatory bias to novel locations. We found no evidence for delayed covert orienting, but such delays might occur in other situations. Likewise, there was no convincing evidence for a facilitatory bias of attention to novel locations in the present study. The N2pc was numerically larger in the change condition than in the neutral condition, but this effect did not approach statistical significance. So although IOR might be associated with these other sorts of attentional modulations in different situations, our study shows that IOR can influence performance in visual-search tasks without any inhibitory delays of attention or any substantial facilitatory bias to novel locations.

The present study advances our understanding of how people search their visual environments and how the neural activity in visual cortex relates to perception and action. Consistent with recent work (McDonald, Teder-Sälejärvi, Di Russo, & Hillyard, 2005), the results reported above show that the timing of our visual perceptions is not closely associated with the timing of neural activity in visual cortex. Despite the well-known delay in reactions to objects appearing at recently attended locations, we found no evidence that covert deployments of attention to previously attended locations are delayed. This makes intuitive sense in light of the proposed role of IOR in the optimization of search (Najemnik & Geisler, 2005; Müller & von Mühlenen, 2000; Klein & MacInnes, 1999; Klein, 1988; Posner et al., 1985; Posner & Cohen, 1984) because a mere delay in shifting attention would not prevent attention from reaching any particular location. On the basis of our ERP findings, we propose that the visual system optimizes search by diverting attention away from recently attended locations in a probabilistic manner. Existing neurocognitive models of IOR and attention (e.g., Prime & Ward, 2006; Houghton, Tipper, Dagenbach, & Carr, 1994) must be modified to incorporate this inhibitory bias.

Acknowledgments

The research reported here was supported by grants from the Natural Sciences and Engineering Research Council of Canada, the Canadian Foundation for Innovation, the British Columbia Knowledge Development Fund, and the Canada Research Chairs program. C. H. is now at Vrije Universiteit Amsterdam, The Netherlands. The authors thank Michael Posner, Vincent Di Lollo, and Joseph Hopfinger for insightful comments.

Reprint requests should be sent to John J. McDonald, Department of Psychology, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada, or via e-mail: jmcd@sfu.ca.

REFERENCES

Berlucchi, G. (2006). Inhibition of return: A phenomenon in search of a mechanism and a better name. *Cognitive Neuropsychology, 23,* 1065–1074.

Cox, R. W., & Hyde, J. S. (1997). Software tools for analysis and visualization of fMRI data. *NMR in Biomedicine, 10,* 171–178.

Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., & Salmelin, R. (2001). Dynamic imaging of coherent sources: Studying neural interactions in the human brain. *Proceedings of the National Academy of Sciences, U.S.A., 98,* 694–699.

Handy, T. C., Jha, A. P., & Mangun, G. R. (1999). Promoting novelty in vision: Inhibition of return modulates perceptual-level processing. *Psychological Science, 10,* 157–161.

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience, 18,* 604–613.

Hopf, J.-M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., et al. (2000). Neuronal sources of focused attention in visual search. *Cerebral Cortex, 10,* 1233–1241.

Houghton, G., Tipper, S. P., Dagenbach, D., & Carr, T. H. (1994). A model of inhibitory mechanisms in selective attention. In *Inhibitory processes in attention, memory, and language* (pp. 53–112). San Diego, CA: Academic Press.

Kiesel, A., Miller, J., Jolicoeur, P., & Brisson, B. (2008). Measurement of ERP latency differences: A comparison of single-participant and jackknife-based scoring methods. *Psychophysiology, 45,* 250–274.

Klein, R. (1988). Inhibitory tagging system facilitates visual search. *Nature, 334,* 430–431.

Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences, 4,* 138–147.

Klein, R. M., & MacInnes, W. J. (1999). Inhibition of return is a foraging facilitator in visual search. *Psychological Science, 10,* 346–352.

Luck, S. J., & Ford, M. A. (1998). On the role of selective attention in visual perception. *Proceedings of the National Academy of Sciences, U.S.A., 95,* 825–830.

Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and

human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology, 33,* 64–87.
Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance, 20,* 1000–1014.
Maylor, E. A., & Hockey, R. (1985). Inhibitory component of externally controlled covert orienting in visual space. *Journal of Experimental Psychology: Human Perception and Performance, 11,* 777–787.
Maylor, E. A., & Hockey, R. (1987). Effects of repetition on the facilitatory and inhibitory components of orienting in visual space. *Neuropsychologia, 25,* 41–54.
McDonald, J. J., Teder-Sälejärvi, W. A., Di Russo, F., & Hillyard, S. A. (2005). Neural basis of auditory-induced shifts in visual time-order perception. *Nature Neuroscience, 8,* 1197–1202.
McDonald, J. J., Ward, L. M., & Kiehl, K. A. (1999). An event-related brain potential study of inhibition of return. *Perception & Psychophysics, 61,* 1411–1423.
Müller, H. J., & von Mühlenen, A. (2000). Probing distractor inhibition in visual search: Inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance, 26,* 1591–1605.
Najemnik, J., & Geisler, W. S. (2005). Optimal eye movement strategies in visual search. *Nature, 434,* 387–391.
Pastötter, B., Hanslmayr, S., & Bäuml, K.-H. (2008). Inhibition of return arises from inhibition of response processes: An analysis of oscillatory beta activity. *Journal of Cognitive Neuroscience, 20,* 65–75.
Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. Bouwhuis (Eds.), *Attention and Performance Vol. X* (pp. 531–556). London: Erlbaum.
Posner, M. I., Rafal, R. D., Choate, L. S., & Vaughan, J. (1985). Inhibition of return: Neural basis and function. *Cognitive Neuropsychology, 2,* 211–228.
Pratt, J., Spalek, T. M., & Bradshaw, F. (1999). The time to detect targets at inhibited and noninhibited locations: Preliminary evidence for attentional momentum. *Journal of Experimental Psychology: Human Perception and Performance, 25,* 730–746.
Prime, D. J., & Ward, L. M. (2004). Inhibition of return from stimulus to response. *Psychological Science, 15,* 272–276.
Prime, D. J., & Ward, L. M. (2006). Cortical expressions of inhibition of return. *Brain Research, 1072,* 161–174.
Reuter-Lorenz, P. A., Jha, A. P., & Rosenquist, J. N. (1996). What is inhibited in inhibition of return? *Journal of Experimental Psychology: Human Perception and Performance, 22,* 367–378.
Spalek, T. M., & Di Lollo, V. (2007). The time required for perceptual (nonmotoric) processing in IOR. *Psychonomic Bulletin & Review, 14,* 327–331.
Tassinari, G., & Berlucchi, G. (1993). Sensory and attentional components of slowing of manual reaction time to non-fixated visual targets by ipsilateral primes. *Vision Research, 33,* 1525–1534.
Taylor, T. L., & Klein, R. M. (2000). Visual and motor effects in inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance, 26,* 1639–1656.
Van Veen, B. D., van Drongelen, W., Yuchtman, M., & Suzuki, A. (1997). Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. *IEEE Transactions on Biomedical Engineering, 44,* 867–880.
Wascher, E., & Tipper, S. P. (2004). Revealing effects of noninformative spatial cues: An EEG study of inhibition of return. *Psychophysiology, 41,* 716–728.
Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature, 400,* 867–869.

This article has been cited by:

1. David J. Prime, Pierre Jolicoeur. 2010. Mental Rotation Requires Visual Short-term Memory: Evidence from Human Electric Cortical ActivityMental Rotation Requires Visual Short-term Memory: Evidence from Human Electric Cortical Activity. *Journal of Cognitive Neuroscience* **22**:11, 2437-2446. [Abstract] [Full Text] [PDF] [PDF Plus]
2. David J. Prime, Patrik Pluchino, Martin Eimer, Roberto Dell'acqua, Pierre Jolicœur. 2010. Object-substitution masking modulates spatial attention deployment and the encoding of information in visual short-term memory: Insights from occipito-parietal ERP components. *Psychophysiology* no-no. [CrossRef]