N1pc reversal following repeated eccentric visual stimulation

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Abstract

Early event-related potential (ERP) hemispheric asymmetries recorded at occipitoparietal sites are usually observed following the sudden onset of a lateral peripheral stimulus. This is usually reflected in an onset-locked larger N1 over the posterior contralateral hemisphere relative to the ipsilateral hemisphere, an early ERP asymmetry labeled N1pc. When the peripheral sudden onset is followed by a central stimulus, or by a bilaterally balanced visual array of stimuli, these events evoke a reversed N1pc, that is, a larger N1 over the hemisphere ipsilateral to the peripheral sudden onset. This N1pc reversal has been taken as evidence for a remapping of the visual space from an absolute, retinally based frame of reference to a relative, attentionally based frame of reference that codes the spatial positions of objects relative to the peripheral sudden onset, rather than relative to the fovea. Here, we pit the reference frame-remapping account against an alternative account based on reduced neural reactivity following the peripheral sudden onset. In three experiments, we varied the spatial location of an object relative to a preceding sudden onset, and tested the opposite predictions generated by the frame-remapping and the reduced neural reactivity accounts. Taken together, the results from the present experiments were consistent with the reduced neural reactivity account and inconsistent with the frame-remapping account.

Descriptors: Visuospatial attention, Spatial coordinates, ERP, N1, N1pc, Neural adaptation

At low-level stages of visual processing, the spatial position of an object is typically coded in eye-centered coordinates, due to the retinotopic organization of the visual system in which nearby points on the retina activate nearby cells in the visual cortex. Such retinotopic coding is still generally preserved as visual processing progresses from striate to extrastriate visual areas (Aguirre, Zarahn, & D'Esposito, 1998; Dell'Acqua, Sessa, Toffanin, Luria, & Jolicœur, 2010; Jack et al., 2007; Zeki, 1993), where neurons with larger receptive fields receive inputs from progressively larger portions of the visual space, potentially including more than just one object. How the visual system represents the spatial arrangement of multiple objects within a visual scene has long been a matter of interest, which has converged on the proposal that configurations of objects can be coded both in absolute, retinotopic coordinates and in relative, object-centered coordinates. This latter coding enables the visual system to represent the position of objects with respect to other objects, or of parts of objects relative to each other, rather than relative to the viewer (e.g., Awh & Jonides, 2001; Jiang, Olson, & Chun, 2000; Jolicœur & Kosslyn, 1983). Retinotopic and object-centered spatial position representations have been proposed to subserve distinct cognitive functions (Neggers, van der Lubbe, Ramsey, & Postma, 2006; Stins & Michaels, 2000), the former primarily involved in action preparation (Goodale & Milner, 1992) and the latter in the generation of viewpointindependent shape representations (Bar, 2003; Marr, 1982; Yamashita, Wang, & Tanaka, 2010). Evidence for the functional and neural dissociability of retinotopic and object-centered spatial coding systems has been reported in behavioral studies with neurologically intact adults (e.g., Corballis, Nagourney, Shetzer, & Stefanatos, 1978; Egly, Driver, & Rafal, 1994; Luo, Lupiáñez, Funes, & Fu, 2010; McMullen & Jolicœur, 1990), with hemineglect patients (e.g., Calvanio, Petrone, & Levine, 1987), with patients suffering from optic ataxia (e.g., Blangero, Khan, Rode, Rossetti, & Pisella, 2011), and in studies based on single-cell recordings and functional magnetic resonance imaging (fMRI), in both primates and humans (Galati, Pelle, Berthoz, & Committeri, 2010; see Colby & Golberg, 1999; Olson, 2003, for reviews).

Moving from a retinotopic to an object-centered frame of reference is consensually held to be controlled by attention mechanisms (Golomb, Chun, & Mazer, 2008). Deploying attention to a visual object makes the attended object the anchor point of a relative spatial frame of reference, with every other object present in the visual field recoded spatially relative to the focus of attention (Danziger, Kingstone, & Ward, 2001; Melcher, 2009; Sapir, Hayes, Henik, Danziger, & Rafal, 2004).

Contrary to past views that frame-remapping of an object's location occurs slowly and only when behaviorally necessary, more recent event-related potential (ERP) evidence suggests that spatial

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Figure 1. Illustration of the frame-remapping and neural adaptation accounts of target-locked N1pc reversal following an eccentric reorienting event. A: A reorienting event (i.e., a lateralized flash) elicits an N1pc response at posterior occipitoparietal sites, with a larger contralateral N1 relative to the ipsilateral N1. B: The frame-remapping account. The spatial coordinates of a central target (blue "X") are coded relative to the preceding reorienting event. A central target now elicits an N1pc of opposite polarity relative to the N1pc elicited by the reorienting event because its spatial position falls in the functional visual hemifield opposite to that occupied by the reorienting event when recoded based on the new frame of reference anchored at the reorienting event. C: The neural adaptation account. Neurons stimulated by the reorienting event receive a more direct and stronger input in the contralateral hemisphere, which causes temporary reduced reactivity of neurons in the contralateral hemisphere relative to the ipsilateral hemisphere contralateral to the reorienting event, reversing the typical N1pc.

remapping may occur rapidly, and to a large extent, automatically. Wascher, Hoffmann, Sänger, and Grosjean (2009) appeared to provide elegant support for this hypothesis. In their study, two identical square placeholders were continuously displayed on the horizontal meridian of a computer screen, to the left/right of an equidistant central fixation cross. On each trial, a bright square appeared randomly at the center of one of the two placeholders, as illustrated in Figure 1A. This brief lateralized flash was hypothesized to attract the focus of attention, thus acting as a *reorienting event*. In two different experiments, the reorienting event was followed by a target stimulus, which was displayed for 50 ms, and consisted of both placeholders changing color (from white to blue; Experiment 1), or in a blue "X" displayed at fixation (Experiment 2). Participants were instructed to ignore the initial reorienting event, and to detect the target onset via key press.

The most important results consisted of two occipitoparietal deflections in the event-related lateralizations (ERLs: contralateral minus ipsilateral waveforms relative to the viewer sagittal body axis) observed in the N1 time range, one time-locked to the leading reorienting event and one time-locked to the trailing target. Brain responses of this type are held to originate from multiple neural generators in the occipitoparietal and occipitotemporal cortices

(Clark, Fan, & Hillyard, 1995), and to be sensitive to attentional modulations via re-entrant signals from prefrontal areas (e.g., Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Hillyard, Mangun, Luck, & Heinze, 1990; Knight, 1997). Importantly, in Wascher et al.'s study (2009), bilateral (Experiment 1) or central (Experiment 2) trailing targets elicited an asymmetrical N1 response that was greater at ipsilateral than at contralateral sites relative to the hemifield in which the initial reorienting event was presented. This imbalance in N1 amplitude has been dubbed N1pc, for N1 posterior contralateral, owing to the similarity with another attentional component reflecting selection of target(s) in multiobject visual displays, namely, N2pc (Brisson & Jolicœur, 2007a, 2007b, 2007c; Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Eimer & Kiss, 2008; Hickey, Di Lollo, & McDonald, 2009; Hilimire, Mounts, Parks, & Corballis, 2009; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006a, 2006b; Kiss, Jolicœur, Dell'Acqua, & Eimer, 2008; Leblanc, Prime, & Jolicœur, 2008; Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994; Mazza & Caramazza, 2011; Robitaille & Jolicœur, 2006).

Wascher et al. (2009) hypothesized that the onset of the reorienting event led to a rapid remapping of spatial coordinates from a retinotopic to an object-based frame of reference anchored at the

location of the reorienting event (Figure 1B). If the spatial coding of subsequent events is reorganized relative to the location of the reorienting event, the functional vertical meridian of the new frame of reference would be centered on the location of the reorienting event, and misaligned with respect to foveally centered retinal coordinates. Moreover, items that are physically balanced in terms of retinal coordinates would be functionally unbalanced with respect to the remapped, object-centered frame of reference anchored at the location of the leading reorienting event. This would produce a greater N1 in the hemisphere contralateral to the remapped hemifield, which would correspond to the hemifield ipsilateral to the reorienting event. Likewise, a retinally balanced stimulus would elicit a lateralized response characterized by an apparent reversal of the typical N1pc in response to trailing central or bilateral target(s), as opposed to the symmetric N1 pattern expected on the basis of retinal coordinates.

Though consistent with the notion that attention may be captured by peripheral salient onsets (e.g., Posner & Petersen, 1990; Yantis & Jonides, 1990), Wascher et al.'s (2009) corollary that attention capture is associated with a rapid remapping of the visual world in object/attention-centered coordinates was based on incomplete evidence, as it lacked a condition in which-following a peripheral reorienting event-target(s) were displayed more eccentrically relative to both the viewer's saggital axis and the reorienting event. Wascher et al.'s (2009) model makes a straightforward prediction for this condition: An N1pc of the same polarity as that triggered by the reorienting event should be observed. Importantly, the inclusion of this condition creates the empirical framework needed to distinguish between the frame-remapping hypothesis and another explanation of Wascher et al.'s (2009) results, which was discussed, but not tested, in the original paper. This alternative account hinges on the interplay between known properties of N1-eliciting neurons in posterior areas, which tend to adapt significantly when stimulated in rapid repetition (Höffken, Grehl, Dinse, Tegenthoff, & Bach, 2008; Kohn, 2007; Spratling, 2011) and the influence of attention-driven re-entrant signals originating in frontal and prefrontal areas under the particular testing conditions designed by Wascher et al. (2009). For ease of exposition, this alternative account will be henceforth referred to as neural adaptation account, and represented in terms of rapid habituation and/or temporary reduced reactivity of N1-eliciting neurons following stimulation by the reorienting event. We will, however, return with a more detailed depiction of the possible sources of this hypothesized, temporary, reduced reactivity of repeatedly stimulated neurons in the General Discussion.

Of note, the neural adaptation model explains Wascher et al.'s (2009) results without the need to postulate rapid remapping between spatial frames of reference. Figure 1C shows how this is possible. The hypothesis is that the presentation of the reorienting event causes a temporary reduction in reactivity in the hemisphere contralateral to the stimulus rather than in the hemisphere ipsilateral to it. Following the reorienting event, a target that would otherwise elicit a symmetric N1 would now produce an asymmetric N1 (i.e., N1pc), with a larger N1 over the hemisphere ipsilateral to the reorienting event that induced neural adaptation. Crucially for the present study, when one considers the presently proposed control condition with target(s) displayed more eccentrically than the reorienting event, the prediction based on the neural adaptation hypothesis is opposite to the prediction from Wascher et al.'s (2009) model: Targets presented in the same (retinotopic) visual hemifield should generally produce a polarity reversal of the N1pc generated by the reorienting event irrespective of whether they are more or less eccentric than the reorienting event. This prediction is simply because targets presented near the adapting event would be affected by the temporary reduced reactivity of the restimulated population of neurons underpinning the N1 response. An aim of the present work was to pit the frame-remapping account proposed by Wascher and colleagues against an alternative neural adaptation account by employing a design that would include the aforementioned critical condition obtained by presenting targets more eccentrically than an attention-capturing reorienting event.

Experiment 1

The key issue in the present work was to provide evidence that would distinguish between the spatial reference frame-remapping and neural adaptation accounts in explaining the patterns of N1pc reversal observed by Wascher et al. (2009). In that study, the target always appeared in a location that should be associated with a reversed N1pc (i.e., larger amplitude at ipsilateral sites) according to the frame-remapping account (Figure 1B), but also according to the N1 adaptation hypothesis (Figure 1C). In Experiment 1, we included a condition in which a target was more eccentric than the reorienting event, such that no N1pc reversal would be expected on the basis of the frame-remapping account, whereas an N1pc reversal would be expected based on the neural adaptation account. The basic design is illustrated in Figure 2. When, according to the frame-remapping account, the remapped coordinates would inverse the ipsilateral-contralateral relationship relative to those based on retinotopic projections, we referred to the condition as nonmatching (i.e., target position less eccentric than the reorienting event). This condition was devised to replicate closely the one used by Wascher et al. (2009). When the target would be coded, according to the frame-remapping account, into the same hemisphere as the reorienting event (i.e., target position more eccentric than the reorienting event), we referred to the condition as *matching*. In other words, the classification of matching versus nonmatching refers to the agreement in spatial coordinates of the reorienting event and following target, assuming rapid remapping of the spatial reference frame.

The configuration of the stimuli on the screen (see Figure 2) and their time course during a trial were very similar to those of Wascher et al. (2009), with the exception that the two matching targets had a greater eccentricity with respect to the reorienting event, and that the nonmatching target appeared below fixationrather than at fixation-in order to control for retinal eccentricity across matching and nonmatching conditions, as well as for the distance between target and reorienting event. The spatial positions of targets were chosen to produce either a reversed N1pc or a typical N1pc according to the frame-remapping account. On the other hand, both matching and nonmatching targets were presented in the same visual hemifield with respect to retinal coordinates, and at the same distance from the reorienting event. On the basis of the neural adaptation account, a reversed N1pc should be evident in response to both matching and nonmatching targets because both were displayed in the spatial proximities of the reorienting event.

Method

Participants. Twelve paid volunteers (aged 20–34, mean age 26.6 years, 9 female) gave informed consent before participating. The data retained for analyses were from all participants, as we had more than two thirds of their trials available following artifact



Figure 2. Stimuli used in Experiment 1 (top panels), Experiment 2 (middle panels), and Experiment 3 (bottom panels). Each graphic reproduction is to scale with the stimuli used in Experiments 1–3. The graphic reproductions do not make explicit that reorienting events and targets were never displayed synchronously on a trial, and that these stimuli—which are reproduced in shades of black—were in fact colored differently when displayed on screen. In Experiment 3, target positions were doubled relative to those in Experiment 2 so as to cover, in line with the proposed design, all possible locations relative to the reorienting event.

rejection. All participants were right-handed, and all reported having normal or corrected-to-normal visual acuity and normal color vision.

Stimuli and procedure. Participants were tested individually, seated in a dimly lit, electrically shielded, and sound-attenuated room, facing a computer screen at a viewing distance of 65 cm, with a response arrow keypad located under their index, middle, and ring fingers. The experiment comprised one practice block of 36 trials followed by 720 experimental trials organized in 12 blocks of 60 trials. Between every block, a display informed participants they had to change the location of the keypad and switch the response hand.

All stimuli were presented on a dark gray background (10 cd/m²). Approximately 600 ms after the onset of the central fixation cross, a white rectangle (54 cd/m²) was displayed for 50 ms. The rectangle acted as reorienting event. The reorienting event subtended a visual angle of 1.2° in width $\times 10.5^{\circ}$ in height, and was horizontally centered 4.4° to the left or right of fixation and vertically centered 4.4° below it.

A colored (blue or red; counterbalanced across subjects) target triangle equiluminant with the background (2.6°) wide at the base and 1.8° high) appeared for 200 ms at a stimulus onset asynchrony (SOA) of 217 ms from the reorienting event. One of the vertices of the target triangle was cut off (notch at upper, left, or right vertex). In the matching condition, this (e.g., blue) triangle appeared on the horizontal meridian in the same hemifield as the reorienting event, at 9.3° from fixation, and symmetrically coupled in the opposite hemifield with a (e.g., red) triangle that had the same dimensions and luminance as the target triangle, but with a different notch vertex. In the nonmatching condition, a single target-colored trian-

gle was displayed on the vertical meridian, 7.8° below fixation. There were 5 equiprobable conditions intermixed at random within each block of experimental trials. In 1/5 of trials, the reorienting event preceded a matching target; in 1/5 of trials, the reorienting event preceded a nonmatching target, and in the remnant 3/5 of trials either a matching target, a nonmatching target, or the reorienting event were presented alone. This resulted in the target appearing in three possible locations: on the vertical meridian of the screen (nonmatching target), more eccentric than the reorienting event (matching target) in the left or right hemifield. Trials where no target was presented were no-go trials. On target-alone trials (i.e., not preceded by a reorienting event), the target positions were still labeled matching/nonmatching to maintain the correspondence across the conditions relative to the reorienting event. Participants were instructed to press the upper, the left, or the right arrow key to indicate the position of the notch on the triangle. The instruction stressed the importance of maintaining central eye fixation throughout the trial and to blink, if necessary, after the response and/or before the beginning of the next trial. Reaction time and accuracy were recorded. Response hand (left vs. right) was changed from block to block for every subject, with counterbalanced orders across subjects.

EEG recording and analysis. The electroencephalogram (EEG) was recorded from 64 Ag/AgCl electrodes (BioSemi ActiveTwo system) placed according to the International 10–10 system at the following sites: Fp1, Fpz, Fp2, AF7, AF3, Afz, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, Poz, PO4, PO8, O1, Oz, O2, and Iz. In addition, two

electrodes were positioned on the mastoids, two electrodes on the outer canthi of the eyes, and one electrode below the left eye. The 64 electrodes were mounted on an elastic cap, and recorded signals were rereferenced to the average of the left and right mastoids during postrecording analyses. Horizontal and vertical electrooculograms (EOG) were computed offline based on activity recorded from electrodes positioned on the external canthi and from electrodes positioned at the Fp1 site and below the left eye, respectively. EEG was recorded at a sampling rate of 512 Hz and low-pass filtered online at 134 Hz. The recorded activity was then high-pass (0.1 Hz, 12 dB/octave) and low-pass (30 Hz, 48 dB/octave) filtered offline with a phase-shift free Butterworth filter.

ERPs were computed for all electrodes by averaging EEG epochs recorded on trials associated with a correct response. Data were screened for artifacts, and epochs with a voltage difference > 100 μ V in a 50-ms time window were excluded from analysis. The same procedure, albeit with different parameters (voltage difference > 40 μ V in a 200-ms time window), was applied to the EOG in order to detect ocular artifacts, and reject the corresponding trials. Epochs time-locked to the onset of the reorienting event were 700-ms long (-100-600 ms), with the preonset 100-ms interval serving as baseline. In order to ensure that eye position did not drift into the area of the stimuli throughout the trial, we analyzed the horizontal EOG channel, dividing the data based on the side that was attended and the experimental condition for each trial. The difference between the residual HEOG signal, averaged separately for left-target and right-target trials, never exceeded 1.9 µV, equivalent to a horizontal eye movement of no more than about .12° of visual angle toward the target (Lins, Picton, Berg, & Scherg, 1993).

Event-related lateralizations (ERLs) were computed for each of the five conditions included in the experimental design by subtracting ipsilateral waves from contralateral waves relative to the retinotopic side of the reorienting event and/or target. Because ERLs were maximal at PO7/PO8 electrodes, statistical analyses focused on data recorded at these electrode sites.

Analyses focused on the P1, N1, and P2 components, and for each component the time window for amplitude estimation was determined through a subjectwise semiautomatic peak detection procedure for ipsilateral, contralateral, and ERL waveforms. N1 responses peaked between 120 and 190 ms after the onset of both the reorienting event and the target. The mean amplitudes of these ERL deflections in the N1 time range were computed as contra minus ipsilateral ERPs within an interval of ± 25 ms relative to the individual peaks. The presence of P1, P2, and relative ERL peaks was similarly ascertained through per-subject peak selection in 40-190 ms and 190-330 ms time windows, that is, in time windows preceding and following the N1 time window. For comparison purposes, time windows for the computation of mean amplitude values where no evoked activity could in principle be recorded (i.e., in trials in which targets or reorienting events were presented alone) were derived from trials in which the relative stimulus was instead presented in the same \pm 25 ms intervals around the peak detected in these trials.

The analysis of unsubtracted ipsilateral and contralateral ERP responses to the targets were performed using an analysis of variance (ANOVA) on data from target-present trials, considering location (matching vs. nonmatching), reorienting event (present vs. absent), and hemifield (contralateral vs. ipsilateral) as withinsubject factors. The mean amplitude of target evoked ERLs were tested against zero by t test for every lateralized component. The analysis of ERL responses to the targets were performed using an ANOVA, considering target location (matching vs. nonmatching) and reorienting event (present vs. absent) as within-subject factors. In all multifactorial analyses, a Greenhouse-Geisser correction was used where appropriate.

Results

Behavior. Reactions times (RTs) to targets were screened for fast guesses (RT < 200 ms) and very slow responses (RT > 1,200 ms), totaling the 0.9% of correct trials that were discarded from both RT and EEG analyses. RTs and error percentages were submitted to ANOVA considering target location (matching vs. nonmatching) and reorienting event (present vs. absent) as within-subject factors.

The ANOVA on mean RTs indicated shorter RTs when the reorienting event preceded the target (544 ms) relative to when the reorienting event was absent (558 ms; F(1,11) = 5.25, p < .05, $\eta^2 = .32$), and longer RTs to matching targets (579 ms) relative to nonmatching targets (523 ms; F(1,11) = 5.25, p < .05, $\eta^2 = .32$). The interaction between these factors did not reach significance (F < 1, p > .23). The overall mean accuracy was 94.9% (SD = 13.73). The ANOVA on error percentages showed no significant effects, all Fs < 3.00, all ps > .07.

Electrophysiology (ERPs and ERLs). The most important results are shown in Figure 3. In each graph, zero on the abscissa indicates the time of onset of the reorienting event, while the vertical line at 217 ms indicates the onset of the target. Consider first Panels C1 and C3, reporting unsubtracted ERPs elicited by targets displayed without a leading reorienting event. Ipsilateral and contralateral ERPs in Panel C3 were computed arbitrarily, given that the target was displayed centrally. ERPs in Panels C1 and C3 showed a clear N1 response for both matching and nonmatching targets. The P1 component was clear for matching targets and indistinct for nonmatching targets. On the other hand, nonmatching trials elicited a more apparent P2 than matching trials. These differences across matching and nonmatching trials likely reflected specific ERP modulations owing to an obvious physical difference between matching and nonmatching targets, for matching targets were always shown with an accompanying balancing stimulus whereas nonmatching targets were singularly presented stimuli (see Figure 2). ERLs in Panel C2 were computed as the contralateral minus ipsilateral difference of the ERPs in Panel C1, while ERLs in Panel C4 were computed as the difference of the ERPs in Panel C3. As expected, the ERLs in Panel C4 were flat in the N1 time range when a single target was presented centrally, while a negativity in the N1/N2 time range can be seen in Panel C2, when only one target of the bilateral-target display was relevant to the task, and had to be selected for further processing based on color (i.e., in the absence of a leading spatial cue represented by the reorienting event that, when present, was always predictive of the side of occurrence of the subsequent target; mean amplitude = $-2.22 \text{ }\mu\text{V}$, t(11) = 5.82, p < .001). The temporal profile of such ERL negativity may be indicative of typical N2pc response elicited by the colored bilateral display, as it may be naturally expected given this is a stimulus/task configuration typically employed to elicit such type of ERL response. As evident in Panel C2, what was therefore captured in the monitored time window was the initial portion of a target-locked N2pc, which is held to be associated with an endogenously driven shift of attention (e.g., Hopf et al., 2000).

Unsubtracted ERPs elicited by the reorienting event displayed in isolation are illustrated in Panel A1 (and reproduced in Panel A3 to facilitate visual comparisons with lower panels). Given that this



Figure 3. ERP/ERL results of Experiment 1. The letters A–E and numbers 1-4 are used to indicate panels in a given row and column, respectively. Legends referring to the experimental conditions (see text for details) are reported on the left side of each row of panels. In each panel, the time scale is locked to the onset of the reorienting event (time = 0 ms), and the onset of the target is indicated in panels B–E by a vertical line (time = 217 ms). Light gray shaded areas in Columns 2 and 4 indicate the time window monitored to detect ERL modulations predicted by the frame-remapping and neural adaptation accounts. R.E. = reorienting event.

stimulus was lateral (as shown in Figure 2), we expected differences across contralateral and ipsilateral responses, reflecting such physical asymmetry. The contralateral P1 was earlier than the ipsilateral P1, with about the same amplitude, whereas the contralateral N1 was both earlier and larger than the ipsilateral N1. ERLs in Panel A2 (reproduced in Panel A4) were computed as the contralateral minus ipsilateral difference of the ERPs in Panel A1. The comparison of Panels A1 and A2 suggests that the apparent P1pc in A2 reflects the earlier contralateral P1, with the following N1pc being the sum of a contralateral N1 and a delayed ipsilateral P1. In addition, a P2pc appears to reflect a greater contralateral P2 relative to the ipsilateral P2. Consider now the ERPs in Panels B1 and B3, which show unsubtracted ERPs elicited in trials when both reorienting event and targets were displayed. Panel B1 shows contralateral and ipsilateral ERPs elicited in trials with a matching target, while Panel B2 shows contralateral and ipsilateral ERPs elicited in trials with a nonmatching target. Panel B2 shows ERLs computed by subtracting the ERPs shown in Panel B1 (matching target trials), and Panel B4 shows ERLs computed by subtracting the ERPs shown in Panel B3 (nonmatching target trials). Unsurprisingly, the initial portions of these ERLs are essentially identical to those from trials in which the reorienting event was presented in isolation (Panels A1 to A4), because-up to the presentation of the targetthese two types of trials had identical stimuli. Following the target onset, however, major differences unfold in the ERLs associated with a target displayed in isolation relative to when the target was preceded by a reorienting event, which are evident in ERLs in Panels C4 and B4. Specifically, a regular N1pc can be seen in the response to the reorienting event and a reversed N1pc (shaded area in Panel B4) can be seen in response to nonmatching targets, thus providing a close replication of Wascher et al.'s (2009) findings.

Consider next the results from trials with both a reorienting event and a matching target, namely, trials restimulating the same physical and functional hemisphere. Recall that the N1pc should not reverse between reorienting event and target according to the frame-remapping account proposed by Wascher et al. (2009). The results in Panel B2, instead, show a clear reversal of the N1pc, which is remarkably similar to the reversed N1pc elicited by nonmatching targets and shown in B4.

Statistical tests were carried out to corroborate the foregoing description of the results. The amplitude of the target-elicited ERL in the N1 time window was significantly different from zero when the target followed a reorienting event, both on matching target trials (Panel B2; mean amplitude = $2.93 \mu V$, t(11) = 4.77, p < .001) and nonmatching target trials (Panel B4; mean amplitude = 2.93 μ V, t(11) = 4.97, p < .001). Notably, matching and nonmatching targets both elicited positive N1 deflections following a reorienting event, suggesting an unequivocal dependency of target-locked N1pc reversals driven by stimulation coded in retinally centered rather than attentionally remapped-spatial coordinates.

A statistical comparison between the data in the posttarget N1 time window shown in Panels B2/B4 and Panels C2/C4 was carried out through an ANOVA that considered target location (matching vs. nonmatching) and reorienting event (present vs. absent) as within-subject factors. The analysis revealed that a significant N1pc reversal was detected when the reorienting event preceded a target (Panels B2/B4; mean amplitude = 2.99μ V), but not when a target was presented in isolation (Panels C2/C4; mean amplitude = $-1.15 \ \mu\text{V}$; F(1,11) = 41.17, p < .0001, $\eta^2 = .79$). The same held true for the reversal of the P2pc into a negative component, which was evident when the reorienting event preceded a target (Panels B2/B4; mean amplitude = $-2.80 \,\mu$ V), but not when a target was presented in isolation (Panels C2/C4; mean amplitude = $0.55 \,\mu\text{V}; F(1,11) = 22.30, \, p < .001, \, \eta^2 = .67).$

ERL amplitudes in the posttarget N1 time window for matching targets (mean amplitude [Panels B2/C2] = $0.36 \,\mu\text{V}$) and nonmatching targets (mean amplitude [Panels B4/C4] = 1.42μ V) differed significantly, F(1,11) = 7.60, p < .05, $\eta^2 = .41$, with this difference, however, depending on the presence/absence of the reorienting event, F(1,11) = 13.09, p < .01, $\eta^2 = .54$. This interaction is further support for the interpretation of one of the t tests reported in the foregoing passages that the significant negative deflection observ357

able in Panel C2 was in fact an early N2pc in response to the target of the bilateral-target display, reflecting selection based on color in the absence of a leading cue where attention could be anchored in anticipation.

The ERLs shown in Panels B2 and B4 are the most important results of Experiment 1. These contralateral minus ipsilateral waves show the combined activity produced by the reorienting event, the target, and the lateralized interaction when both were shown in rapid succession. A succinct way to visualize this interaction can be achieved through a two-step process of waveform subtraction. Firstly, ERPs recorded in trials when the reorienting event was displayed in isolation were subtracted from ERPs recorded in trials with reorienting event plus target. The panels labeled with Ds in Figure 3 show the results of this first step. Secondly, ERPs recorded in trials when a target was displayed in isolation were subtracted from ERPs resulting from the first-step subtraction. Conceptually, this double subtraction removes ERP activity generated by the reorienting event and target when presented in isolation from ERPs recorded in trials when both stimuli were displayed on the same trial, leaving as a residual ERP activity reflecting the net effect of the interplay between reorienting event and target when displayed in close temporal succession.

These results, shown in Panels E1 to E4 of Figure 3, provide further corroborating evidence for the neural adaptation account vis-à-vis the frame-remapping account proposed by Wascher et al. (2009). A close replication of Wascher et al.'s (2009) results is reported in Panel E4, where the ERL is characterized by a pattern of N1pc reversal in trials when the reorienting event was trailed by a nonmatching target. A strikingly similar pattern can be observed in Panel E2, showing the ERL generated considering trials when the reorienting event was trailed by a matching target. In the posttarget N1 range, the ERL deflections shown in Panels E2 and E4 were identical quantitatively (both mean amplitudes: $2.27 \mu V$), and did not differ statistically, t(11) = 1.06, p > .30.

Discussion

As found by Wascher et al. (2009), when a balanced target display followed a lateral reorienting event, and the target was less eccentric than the reorienting event, a reversed N1pc was found in response to the target. This finding is consistent with a possible rapid remapping of the visual space following the reorienting event. A target presented at a more eccentric location than the reorienting event, however, would not have remapped spatial relations relative to the new reference frame postulated by Wascher et al. (2009). According to the frame-remapping account, therefore, this condition should have produced a typical N1pc rather than a reversed N1pc. A reversed N1pc was instead expected in this condition based on the neural adaptation account, because adaptation should affect equally more and less eccentric target positions as long as both are displayed in the same retinotopic visual hemifield. The results were clear-cut in showing that, when preceded by a reorienting event, more eccentric targets, like less eccentric targets, produced a reversed N1pc, in line with the neural adaptation account.

Further support to the neural adaptation account derives from the isolation of the ERL waveforms reflecting the interaction between the eccentric reorienting event and matching and nonmatching targets, which was obtained through a two-step subtraction illustrated above (Figure 3, Panels E1-E4). Here, the same pattern of interaction with matching and nonmatching targets was observed, indicating that the spatial relations between the location of the target and preceding reorienting event produced neither qualitative nor quantitative difference in how the presentation of the preceding event affected the posttarget ERLs in the N1 range, a result that the frame-remapping account cannot easily explain as presently formulated.

Experiment 2

One concern in Experiment 1 was that our matching-target condition included two lateral notch triangles displayed in opposite hemifields, one of which in particular, the nontarget, was always in a nonmatching position relative to the initial reorienting event. Perhaps activation from the nontarget triangle attenuated the expected frame-remapping response to the target triangle, obscuring the results expected on the basis of the frame-remapping hypothesis.

Another way to phrase this possible concern is that the matching-target condition in Experiment 1 had a distractor that was at a greater distance from the reorienting event than the target, and one might be concerned that this would create more signal on the distractor side of the reorienting event than on the target side, which might override the initially balanced display. Although prior work suggests that the closer stimulus to the hypothetical new functional (remapped) fixation would outweigh the farther one, as argued and supported by, for example, the work of Woodman and Luck (2003), Experiment 2 was specifically designed to control for this possible confound, using lateral targets presented in one visual hemifield that were not balanced by a distractor in the other hemifield. This produced displays that were equally unbalanced in the matching and nonmatching conditions, as illustrated in Figure 2.

The predictions based on the frame-remapping account proposed by Wascher et al. (2009) were the same as those derived for Experiment 1. Targets preceded by a reorienting event displayed in the close spatial proximities should elicit a "normal" N1pc when displayed in matching position (i.e., more eccentrically than the reorienting event), and a reversed N1pc when displayed in a nonmatching position (i.e., less eccentrically than the reorienting event). The predictions based on the neural adaptation account, in contrast, are to be reframed in light of the results from Experiment 1 while considering the difference in the spatial organization of the stimuli used in Experiment 2. Specifically, whereas in Experiment 1 a reversal of the N1pc could be expected for nonmatching targets by virtue of the subtraction between a target-locked N1 response of reduced amplitude in the hemisphere contralateral to the reorienting event and a normal N1 response recorded from the not previously stimulated hemisphere, targets in Experiment 2 were always displayed in the same visual hemifield as that occupied by the reorienting event. This yields to the prediction that-rather than a reversal of N1pc in response to both matching and nonmatching targets-the expected pattern should be one of an N1pc of reduced amplitude in response to targets when preceded by a reorienting event. Crucially, however, this reduced N1pc should not differ between matching and nonmatching targets, as both should be equally affected by the preceding presentation of the reorienting event.

Method

Participants. Seventeen paid volunteers (aged 19–26, mean age 21 years, 9 female, 2 left-handed) gave informed consent before participating in the experiment. Artifact rejection resulted in the exclusion from analyses of the data from five of them. Results were

based on the remaining 12 participants. All participants reported having normal or corrected-to-normal visual acuity and color vision.

Stimuli and procedure. Experimental stimuli and procedure in Experiment 2 were like those in Experiment 1, with a few exceptions (see Figure 2). An always-blue notched target triangle was presented either in matching or nonmatching locations, but the matching target configuration no longer included a balancing nontarget displayed in the opposite visual hemifield. Additionally, nonmatching targets appeared now in a new location so as to keep constant both the distance between each target triangle and the preceding reorienting event and the distance of each target triangle from central fixation. The reorienting event was presented farther from fixation (7.2° in Experiment 2 vs. 4.4° in Experiment 1), and the nonmatching target, which was previously displayed centrally below fixation, was moved closer to the reorienting rectangle. Thus, all targets in Experiment 2 consisted of identical triangles, equiluminant to the background, as well as equidistant both from fixation (9.3°) and reorienting event (1°) .

As in Experiment 1, participants were asked to press the upper, the left, or the right arrow key, to indicate the position of the notch on the triangle. In 1/3 of the trials, the reorienting event was displayed alone (no-go trials); in 1/3 of the trials, the target was presented alone; and in 1/3 of the trials, both the reorienting event and the target were sequentially presented at the same SOA used in Experiment 1. When the target was presented, it could be in a matching (50% of go trials) or nonmatching (50% of go trials) location. Therefore, the design included the same five equiprobable conditions of Experiment 1: reorienting event and matching target trials, no reorienting event and matching target trials, no reorienting event and nonmatching target trials, and trials in which the reorienting event was not followed by a target.

As in Experiment 1, participants were instructed to change the response hand at the end of each block, and the order of blocks was counterbalanced across participants. All other conditions were otherwise intermixed at random within each block of trials.

Results

Data from five participants were excluded from analyses because more than 33% of the total trials were discarded by artifact rejection criteria. Two of them were rejected due to excessive blinking, one because of a very high proportion of trials with high-amplitude alpha waves, and one because of low signal-to-noise ratio. One participant had an error rate that was more than twice that of the other participants.

Behavior. Behavioral analyses were identical to those of Experiment 1, with the exception that a further factor was added to the design of the ANOVA because, contrary to what happened in Experiment 1, nonmatching targets could now appear either in the left or in the right hemifield, covarying with the side of presentation of the reorienting event.

Fast guesses (RT < 200 ms) and very slow responses (RT > 1,200 ms), representing 1.1% of the correct trials, were discarded from analyses. Error percentages and RTs were submitted to ANOVA considering target hemifield (left vs. right), target location (matching vs. non-matching), and reorienting event (present vs. absent) as within-subject factors.

The ANOVA indicated shorter RTs when the reorienting event preceded the target (566 ms) relative to when the reorienting event was absent (588 ms; F(1,11) = 15.42, p < .0025, $\eta^2 = .58$). There were no other significant effects on RTs (all *Fs* < 2.12, all *ps* > .17). The mean accuracy was 95.3% (*SD* = 12.14). The ANOVA on error percentages showed no significant effects (all *Fs* < 2.39, all *ps* > .16).

Electrophysiology (ERPs and ERLs). ERPs for each of the five conditions, for ipsilateral, contralateral, ERL waves, are shown in Figure 4. Panels C1 and C3 of Figure 4 show that, differently from Experiment 1, where a balanced visual stimulus was presented, an N1 response occurred contralaterally to the hemifield in which only the target was presented, and propagating ipsilaterally later in time and reduced in amplitude. Importantly, as in Experiment 1, responses to matching targets (Panel C1) did not differ from responses to nonmatching targets (Panel C3). Matching target trials (Panels B1 and C1; mean amplitude = 5.56μ V) showed bigger P1 peaks, F(1,11) = 14.64, p < .01, $\eta^2 = .57$, than nonmatching target trials (Panels B3 and C3; mean amplitude = 4.53μ V). Matching target trials (Panels B1 and C1; mean amplitude = -2.58μ V) showed reduced N1 amplitudes, F(1,11) = 30.49, p < .001, $\eta^2 = .74$, with respect to nonmatching target trials (Panels B3 and C3; mean amplitude = -4.81μ V). These results suggest slightly more positive ERPs elicited by matching targets in the P1/N1 time range, probably due to slightly different response properties of neurons for different target locations.

A Hemisphere × Reorienting Event two-way interaction effect, F(1,11) = 6.59, p < .05, $\eta^2 = .38$, was also observed in the N1 time range. Tukey's HSD post hoc pairwise comparisons (p < .05) indicated that target-elicited contralateral N1 deflections were significantly more negative than ipsilateral deflections only when targets were presented in isolation (Panels C1 and C3; mean amplitude contralateral = -5.78μ V, mean amplitude ipsilateral = -2.99μ V), whereas ERPs recorded from the two hemispheres did not differ (p > .05) when the target was preceded by the reorienting event (Panels B1 and B3; mean amplitude contralateral = $-3.62 \text{ }\mu\text{V}$, mean amplitude ipsilateral = $-2.34 \text{ }\mu\text{V}$). This latter effect was responsible for the observed N1pc attenuation in those trials where the reorienting event was presented before the target. ERLs in Panel C2 were computed as contralateral minus ipsilateral ERPs in Panel C1, whereas ERLs in Panel C4 were computed as contralateral minus ipsilateral ERPs in Panel C3.

Lateralized components peaked at approximately the same latencies in every condition, which coincided with the latencies of the reversed P1pc, N1pc, and P2pc observed in Experiment 1 (from target onset: P1pc = 96 ms; N1pc = 151 ms; P2pc =210 ms). On trials when the reorienting event was presented, the amplitude of each investigated component of the ERLs differed from trials in which the reorienting event was not presented. More precisely, the P1pc was enhanced, F(1,11) = 11.76, p < .006, $\eta^2 = .52$, by the presence of the reorienting event (Panels B2 and B4 [reorienting event present]; mean amplitude = $5.01 \,\mu$ V; Panels C2 and C4 [reorienting event absent]; mean amplitude = 2.64μ V). In contrast, the N1pc was of reduced amplitude, F(1,11) = 35.70, p < .0001, $\eta^2 = .76$, when the reorienting event preceded the target (Panels B2 and B4 [reorienting event present]; mean amplitude = -3.20μ V; Panels C2 and C4 [reorienting event absent]; mean amplitude = -6.30μ V), like the trailing P2pc pattern of responses, F(1,11) = 19.62, p < .0011, $\eta^2 = .64$, (Panels B2 and B4 [reorienting event present]; mean amplitude = $0.48 \,\mu$ V; Panels C2 and C4 [reorienting event absent]; mean amplitude = $4.30 \,\mu\text{V}$).

Crucially for the present test, there were no effects, F(1,11) = 0.67, p > .43, of target location (Panels B2 and C2 [matching targets]; mean amplitude = -4.97μ V; Panels B4 and C4 [nonmatching targets]; mean amplitude = -4.53μ V), nor of the interaction between target location and reorienting event in the N1 range of the ERL. That is, attenuated N1pc responses to matching and nonmatching targets did not differ significantly, in line with predictions from the neural adaptation account.

ERLs were submitted to the two-step subtraction described for Experiment 1, and the results are summarized in Figure 4. Residual (i.e., isolated via subtraction) activity in the N1 range that we had ascribed as net interactive effects between reorienting event and matching versus nonmatching target was characterized by identical polarity, with residual amplitudes (Panel E2; mean amplitude = $2.75 \,\mu$ V and Panel E4; mean amplitude = $3.11 \,\mu$ V) that did not differ significantly, *t*(11), *p* > .71.

Discussion

The size of the predicted N1pc attenuation produced by the reorienting event was the same for matching and nonmatching targets, and the isolated ERLs reflecting the interaction between reorienting event and matching and nonmatching targets were unequivocally identical (see plots E2 and E4, Figure 4). Experiment 2 provided therefore a replication and an extension of the most important findings of Experiment 1 to a stimulus configuration that we devised to solve a class of problems potentially related to the presentation of bilateral stimuli in the matching target condition of Experiment 1. In fact, an interesting difference between the two experiments can be found at the level of the simpler waveforms just because targets were part of physically balanced displays in Experiment 1, but not in Experiment 2. A direct comparison between Panels C1 and B1 and between Panels C3 and B3 in Figure 4 reveals that when the target followed the reorienting event it elicited an N1 response that was contralaterally reduced, and the size of this asymmetric reduction was enough to bring the amplitude of the contralateral visual response at the level of the ipsilateral one. This explains, on the one hand, why the basic N1pc was not actually reversed in Experiment 2 and, on the other, the reason for the N1pc reversal highlighted by Wascher et al. (2009), and replicated in Experiment 1. Accordingly, adaptation effects following the reorienting event were clearly present in the doublesubtraction waves (Panels E2 and E4, in Figure 4), and reflected a greater adaptation (i.e., temporary reduced reactivity) in the hemisphere contralateral to the reorienting event, converging nicely with the results of Experiment 1 (Panels E2 and E4, in Figure 3).

Experiment 3

The logic of Experiment 2 as a test of the remapping hypothesis rests heavily on the assumption that the position of the targets relative to the reorienting event was easy to perceive. If participants could not perceive that the target was to the left or right of the reorienting event, then it would not be surprising if evidence for spatial remapping would not surface in a corresponding ERP manifestation. There are logical arguments that make this potential unlikely. For instance, if the visual system could not code target position relative to the reorienting event because of the reduced spatial resolution in the visual periphery (vs. foveal vision), then it is not clear why one should ever observe a reversed N1pc. In addition, should the spatial position of the targets be perceptually



Figure 4. ERP/ERL results of Experiment 2. The letters A–E and numbers 1–4 are used to indicate panels in a given row and column, respectively. Legends referring to the experimental conditions (see text for details) are reported on the left side of each row of panels. In each panel, the time scale is locked to the onset of the reorienting event (time = 0 ms), and the onset of the target is indicated in panels B–E by a vertical line (time = 217 ms). Light gray shaded areas in Columns 2 and 4 indicate the time window monitored to detect ERL modulations predicted by the frame-remapping and neural adaptation accounts. R.E. = reorienting event.

"confused" with that of the reorienting event, then the remapping account should predict that absence of any form of N1pc-like response, as reorienting event and targets would share largely overlapping spatial coordinates.

Logical arguments aside, in order to ascertain whether the spatial position of the target could be perceived as distinct from that

of the reorienting event, we designed Experiment 3 as a control experiment in which participants were instructed to classify, as quickly as possible while keeping errors to a minimum, targets as left or right relative to the peripheral reorienting event. Stimulus size, retinal position, and timing parameters were identical to those used in Experiment 2, except for the addition of four new positions

 Table 1. Results of Experiment 3

Target horizontal location	Matching	Nonmatching
Target vertical location		
Upper	358 (2.0%)	392 (3.0%)
Lower	364 (3.6%)	373 (1.6%)

Notes. Mean reaction time (and % of errors) as a function of target location relative to the horizontal displacement (target horizontal location) and vertical extension (target vertical location) of the reorienting event as displayed on screen (see Figure 2).

to enable an unbiased test of the perception of the left/right target location all along the vertical extension of the reorienting event (see Figure 2).

Method

Participants. Six paid volunteers (aged 21–26, mean age 24.0 years, 4 female, all right-handed) gave informed consent before participating in the experiment. All participants reported having normal or corrected-to-normal visual acuity and color vision.

Stimuli and procedure. The stimuli and timing parameters were the same as in Experiment 2, except for the addition of four new target locations (two in each visual hemifield), as illustrated in Figure 2 (bottom row). The new positions were in left-right mirror symmetry about the reorienting event in the original matching and nonmatching target locations of Experiment 2. On each trial, a lateral reorienting event was presented, followed by a target at one of the four possible locations surrounding the reorienting event, and the task was to indicate whether the target was to the left/right of the reorienting event, as quickly as possible while making as few errors as possible. Responses were made by button press, with stimulus/response mapping counterbalanced across subjects. Each participant began with 24 practice trials followed by 480 experimental trials organized in 10 blocks of 48 trials. Each block contained an equal number of randomly ordered trials generated by the orthogonal variation of the two locations of the reorienting event (left/right relative to central fixation) with the four possible target locations (two left vs. two right). As in Experiments 1 and 2, in order to ascertain that eye position did not drift into the area subtended by the target stimuli, we analyzed residual horizontal EOG data in each of the cells of the present design based on trials associated with a correct response. Residual HEOG signal never exceeded 2.3 µV, equivalent to a horizontal eye movement of no more than about .14° of visual angle toward the target (Lins et al., 1993).

Results

RTs were screened for outliers using the procedure described in Oriet, Tombu, and Jolicœur (2005), which resulted in the loss of 1.4% of the correct trials. Correct RTs were averaged for each participant and condition. The results are shown in Table 1. An ANOVA carried out on individual RT and accuracy values indicated no significant factor effects (all Fs < 1).

Discussion

As can be seen in Table 1, accuracy in the task was very high, and response times were shorter than 400 ms in all conditions. These

results show that participants could easily perceive the relative location of the target with respect to the preceding reorienting event. Given that the targets in Experiment 1 were more distant from the reorienting event and less eccentric than in Experiments 2 and 3, the present results show that our experimental conditions permitted rapid spatial coding of the target-reorienting event spatial relation, ruling out spatial confusion as a critical determinant of the pattern observed in both Experiments 1 and 2.

General Discussion

When central and bilateral targets appear in a sensory balanced display, shortly after the presentation of a lateralized peripheral stimulus, they produce what may appear to be a lateralized response at occipitoparietal electrodes with unusual characteristics (Wascher et al., 2009). Rather than a typical, symmetric N1 response, the postperipheral stimulus produces an asymmetric N1pc response of polarity opposite to that generated by the leading lateralized peripheral stimulus. It has been proposed that this N1pc reversal might reflect a rapid reorganization of visual processing in which stimulus locations are coded relative to the focus of attention, deployed to the lateralized stimulus, rather than relative to retinal coordinates. Depending on the relative location of the stimuli and the preceding lateralized attention-orienting event, a mechanism of relative spatial recoding could be responsible for the reversal in the polarity of the N1pc (Wascher et al., 2009). The alternative account proposed in the present context predicts that the lateralized landmark reorienting event causes greater adaptation in populations of neurons in contralateral cortical visual areas than in ipsilateral cortical areas, thus differentially impairing subsequent responses to targets displayed in close temporal and spatial contiguity to the attention-capturing reorienting event.

In two experiments, the effect of peripheral cueing on targetelicited ERLs was explored in a discrimination task. A white rectangle was displayed for 50 ms and was followed at an SOA of 217 ms by a central or bilateral (Experiment 1) target stimulus, or by a lateralized target (Experiment 2). The aim of the study was to test predictions of the visual frame-remapping account for the reversal of N1pc and those of the lateralized adaptation account, using stimulus conditions designed to distinguish between them. In Experiment 1, we adapted the original design of Wascher and colleagues (2009) so as to provide both a conceptual replication of their effects as well as tests of the competing explanation. Most importantly, our experiment included a manipulation of the spatial location of the targets relative to the previously flashed reorienting event. The target could be on either side of the leading reorienting event so as to result either in a reversal of spatial coordinates, or not, on the assumption that a new reference frame was established at the location of the initial stimulus. The results were clear-cut: A reversal of N1pc was observed regardless of the spatial location of the target relative to the attention-capturing reorienting event, disconfirming a major prediction of the frame-remapping account. On the other hand, the results were predicted by the neural adaptation explanation in that the reversal of the N1pc appeared to result from the presentation of a balanced visual stimulus to a visual system in a state of physiological/functional reactivity imbalance owing to the momentary adaptation of contralateral neurons in response to the initial reorienting event, which makes it quite straightforward to explain why matching and nonmatching targets were equally associated with a reversal of N1pc.

Experiment 2 extended the results of Experiment 1 by using target displays that always consisted of a single target, which now

produced an adapted regular N1pc as a result of the absence of a nonadapted ipsilateral response to unbalanced target displays. Moreover, because of the addition of other conditions in the experiment, namely, initial flash alone, target alone, and flash plus target, the design enabled a further test of the two opposing accounts. As in Experiment 1, the location of the target was varied so as to produce different spatial codings relative to the initial reorienting event, which should have produced a reversal of N1pc in one case and a normal, not reversed, N1pc in the other. These locations were at the same distance from the reorienting event, and thus should have been equally susceptible to neural adaptation. As can be seen in Figure 4, neither condition produced a reversal of N1pc. However, relative to the target-alone conditions, and consistently with the neural adaptation account, the presence of a leading reorienting event reduced both matching and nonmatching targetlocked N1pc amplitudes much in the same way. In Experiments 1 and 2, we estimated the stimulus interaction that produced the N1pc reversal by subtracting the nonadapted response to the target and the response to the reorienting event from the response to the combined stimulus (flash plus target), as can be seen in the last rows of Figures 3 and 4. Indeed, these responses were unaffected by the location of the target relative to the reorienting event, and were nearly identical in polarity and magnitude. Experiment 3 complemented the results of Experiments 1 and 2 by showing that the relative position of the targets with respect to the reorienting event could be perceived with immediacy, minimizing therefore the probability that the results of Experiments 1 and 2 were contaminated by sensory factors referred to a reduction in spatial resolution owing to the eccentricity of the stimulus configuration.

As a whole, the electrophysiological results in both Experiments 1 and 2 show that the observed unbalanced neural response produced by central or bilateral peripherally cued targets in visual areas appears to be due to selective hemispheric adaptation following the presentation of a lateralized adapting stimulus (i.e., the reorienting event). Although there is clear evidence that a peripheral flash can attract attention to its location (e.g., Posner, 1978), this does not appear to be necessarily symptomatic of a change from a retinotopic to an object-centered spatial coordinates system. It is likely that attention drawn to the reorienting event also modulated the ERP of the target, probably by enhancing the overall amplitude of the P1 and N1 components (Mangun, 1995). Importantly, this effect would not depend on which side of the reorienting event we presented the target. Perhaps riding on top of a general attentional enhancement, our results suggest there is greater adaptation in the hemisphere contralateral to an adapting stimulus than in the ipsilateral hemisphere, presumably because of the direct input to the former and indirect input to the latter. The asymmetric visual adaptation in the N1 range is large, and needs to be taken into account in studies of visual attention in which stimuli are presented in rapid succession.

In the foregoing discussion, we argued that a reversed N1pc caused by a stimulus presented at a physically less eccentric spatial location than a preceding reorienting event provides only equivocal evidence for the remapping hypothesis proposed by Wascher et al. (2009). The main reason is that the reversed N1pc is compatible with other explanations, such as sensory adaptation that can be seen, for example, in studies of paired-pulse adaptation (e.g., Höffken et al., 2008). A minimal test of the remapping hypothesis thus requires that one also tests spatial locations relative to the reorienting event that would not cause a reversal of ipsilateral and contralateral directions in the remapped space. Stimuli presented at these locations should not produce a reversed N1pc because there

has been no reversal of the ipsilateral and contralateral directions in the hypothesized remapped space. Together, the reversed N1pc for reversed (nonmatching) ipsicontralateral directions and the normal N1pc for not-reversed (matching) ipsicontralateral directions appear at present to be necessary conditions, at least from a logical perspective, for any test of the remapping hypothesis.

The neural adaptation hypothesis put forth in this context considers a type of local interstimulus interaction, namely, repeated visual stimulation displayed eccentrically, which is common to a range of paradigms testing spatial attention. An effort to form a theoretical generalization of our proposal and functional characterization of the underpinning mechanisms is therefore in order. The visual N1 component has multiple generators that can be differentially affected by a variety of factors (e.g., Makeig et al., 1999), including bottom-up sensory inhibition (e.g., Höffken et al., 2008), top-down attentional effects (e.g., Hillyard & Anllo-Vento, 1998; Mangun, 1995), and task-set effects (e.g., Vogel & Luck, 2000). Furthermore, some of these effects are different for ipsilateral and contralateral electrode sites relative to the stimulated visual field when the stimulus is presented in a lateral visual field location. Considering the time scale of the N1 effects described herein, it becomes hard to look at such effects as confined to early local neuronal interactions triggered in a purely bottom-up fashion, especially in light of recent evidence suggesting that top-down effects on early stages of visual processing, including selection of relevant information, have a much earlier temporal origin than previously thought (Katsuki & Constantinidis, 2012; Wascher & Beste, 2010a, 2010b). The presently proposed account can, however, easily accommodate a late, attention-related, functional origin of what we have been referring to as temporary reduced reactivity of repeatedly stimulated neurons, based on evidence strongly suggestive of competitive (i.e., inhibitory vs. excitatory) interactions as complementary mechanisms enabling target selection, both in visual search (Hilimire, Hickey, & Corballis, 2012; see also Hickey et al., 2009) and inhibition of return (McDonald, Hickey, Green, & Whitman, 2008; Zhang, Zhou, & Zhang, 2012) domains. The suggestion that appears to emerge from these studies is that of a consistent link between inhibition/excitation of neurons in the occipitoparietal cortex (e.g., Prime & Jolicœur, 2009) and the polarity of ERP components held to reflect the activity of such neurons. More specifically, these findings suggest that target activation enhancement is often reflected in a contralateral increment in negativity accompanied by an increment in positivity, held to reflect suppression, contralateral to distractors when such stimuli are displayed in distinct visual hemifields, with these reflections usually unfolding in a 80-300 ms time range after eliciting stimulus (Fortier-Gauthier, Dell'Acqua, & Jolicœur, 2013; Hickey et al., 2009; Sawaki & Luck, 2010), giving rise to N1-N2pc ERLs as those described in the present circumstances. In addition, a contralateral posterior positivity in a window of 130-160 ms, coined Ppc, is also often observed when a salient stimulus is presented in one hemifield accompanied by a luminance-matched distractor in the other hemifield (e.g., Corriveau et al., 2012). When eccentric target and distractor pairs project to different hemispheres (or when target or distractor produce an asymmetric distribution of processing load, such as when either of them is displayed centrally and the other eccentrically), such polarity differential can be decoupled. We note that, in our paradigm, as well as in Wascher et al.'s (2009), the reorienting event was a task-irrelevant stimulus, providing no information about any task-relevant dimensions of the target and, in this vein, it was a distractor in all respects. In this perspective, that a target presented in the same visual hemifield as the leading

reorienting event elicited what appeared to be a reduced negativity may become less surprising, because the (distracting) reorienting event is held to trigger an increase in positivity in the contralateral hemisphere lasting from 80 ms to 300 ms postreorienting event. Interestingly, the SOA between reorienting event and target in Wascher et al.'s (2009) and present studies was about 200 ms, which is a time point falling in the 80–300 ms time window of increased contralateral positivity trailing the reorienting event. As presently reframed, the neural adaptation account of the present findings finds its support in the direct comparison of Panels B1 and C1 in both Figures 3 and 4, where one can see that contralateral ERP deflections elicited by targets following a reorienting event are clearly more positive (Panel B1s) than contralateral ERPs elicited by targets displayed alone (Panel C1s). In conclusion, we reiterate that our objective was not that of disproving the general idea of a top-down and/or attentional nature of the observed effects, but to present results challenging a specific corollary of prior proposals put forth in the spatial attention field; that is, that a reversal in polarity of one specific component, the N1pc time-locked to the onset of a target trailing an eccentric abrupt onset, could be taken, in and of itself, as the hallmark of a rapid shift in spatial frame of reference, from retinotopic to object-centered, used to code object locations in mental representations. The present evidence challenges this interpretation of the N1pc reversal, and is consistent with the persistence of retinotopic mappings of the spatial location of objects in visual working memory following eye movements (Dungan & Vogel, 2012; Golomb & Kanwisher, 2012).

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