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Nasotemporal ERP differences: evidence for increased inhibition of temporal distractors

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Huber-Huber C, Grubert A, Ansorge U, Eimer M. Nasotemporal ERP differences: evidence for increased inhibition of temporal distractors. *J Neurophysiol* 113: 2210–2219, 2015. First published January 14, 2015; doi:10.1152/jn.00344.2014.—Previous research has demonstrated behavioral advantages for stimuli in the temporal relative to the nasal visual hemifield. To investigate whether this nasotemporal asymmetry reflects a genuinely attentional bias, we recorded event-related potentials in a task where participants identified a color-defined target digit in one visual hemifield that was accompanied by an irrelevant distractor in the opposite hemifield (*experiment 1*). To dissociate the processing of stimuli in nasal and temporal visual hemifields, an eye-patching procedure was used. Targets triggered N2pc components that marked their attentional selection. Unexpectedly, these N2pc components were larger and emerged earlier for nasal relative to temporal targets. *Experiment 2* provided evidence that this nasotemporal asymmetry for the N2pc is linked to an increased attentional inhibition of temporal distractors. Relative to nasal distractors, temporal distractors elicited an increased inhibition-related contralateral positivity, resulting in more pronounced differences between contralateral and ipsilateral event-related potentials on trials with temporal distractors and nasal targets. These results provide novel evidence for a genuinely attentional contribution to nasotemporal asymmetries and suggest that such asymmetries are associated with top-down controlled distractor inhibition.

attention; visual hemifield; nasotemporal asymmetry; event-related potentials; N2pc; inhibition

IN THE HUMAN VISUAL SYSTEM, two anatomically distinct pathways propagate input from the retina to the brain. Both retinogeniculate pathways to the lateral geniculate nucleus (LGN) of the thalamus as well as retinotectal pathways to the superior colliculus (SC) in the tectum consist of projections that cross and projections that do not cross the midline of the human brain. Uncrossed projections remain in the same hemisphere as the visual field of stimulation, and crossed pathways project to the contralateral hemisphere. In humans, behavioral differences between crossed and uncrossed neural pathways have been investigated with eye-patching procedures (e.g., Posner and Cohen 1980). When one eye is patched, crossed and uncrossed pathways can be separated by presenting visual stimuli to different hemifields. For instance, if the left eye is patched, a stimulus in the left hemifield appears in the nasal field, is represented on the temporal hemiretina of the unpatched right eye, and is then projected via the uncrossed pathway to the right SC, LGN, and cortical hemisphere. In contrast, if the same left eye is patched but a stimulus is shown to the right, it appears in the temporal visual field, is represented on the nasal hemiretina of the unpatched right eye, and is then projected via the crossed pathway to the left SC, LGN, and cortex (see Fig. 1).

Studies using such an eye-patching procedure have revealed differences in the processing of input from the nasal compared with the temporal visual field (nasotemporal asymmetries). In probably the first study on such asymmetries, Posner and Cohen (1980) showed in a choice saccade task that humans preferentially orient toward signals in the temporal compared with the nasal hemifield. Subsequently, a similar temporal hemifield advantage has been replicated for manual response times (RTs) and saccade latencies, suggesting that cues in the temporal visual hemifield are more efficient in attracting attention, as reflected by larger spatial cueing effects (Rafal et al. 1991). Other studies failed to demonstrate nasotemporal asymmetries for saccade latency (Bompas et al. 2008; Jóhannesson et al. 2012) but confirmed Posner and Cohen's initial observation that a higher proportion of saccades is directed to temporal compared with nasal stimuli (Bompas et al. 2008). Nasotemporal asymmetries have also been demonstrated for interference effects by irrelevant distractors. Rafal et al. (1990) and Walker et al. (2000) demonstrated more interference by task-irrelevant distractors in the temporal hemifield than in the nasal hemifield.

The temporal hemifield advantage has been interpreted in terms of an attentional effect (e.g., Rafal et al. 1991). According to this explanation, a temporal target attracts more attention than a nasal target. However, because many studies have measured eye movements toward target stimuli (e.g., Bompas et al. 2008), it is also possible that the nasotemporal asymmetry reflects a postattentional motor bias (cf. Simon 1969; De Jong et al. 1994). According to the motor explanation, the nasotemporal asymmetry would reflect a bias in favor of directing a motor action toward a temporal stimulus than a nasal stimulus (Ansorge 2003). In the present study, we investigated whether the temporal visual field advantage is indeed linked to attentional biases, the nature of these biases, and the point in time at which they emerge. We focused on the N2pc component of the event-related potential (ERP) as an established electrophysiological marker of attentional target selection to provide direct and unequivocal evidence for a genuinely attentional nasotemporal asymmetry. The N2pc is an enhanced negativity that is elicited at posterior electrodes contralateral to the visual field of a target object in multistimulus visual displays. This component typically emerges around 200 ms after the stimulus

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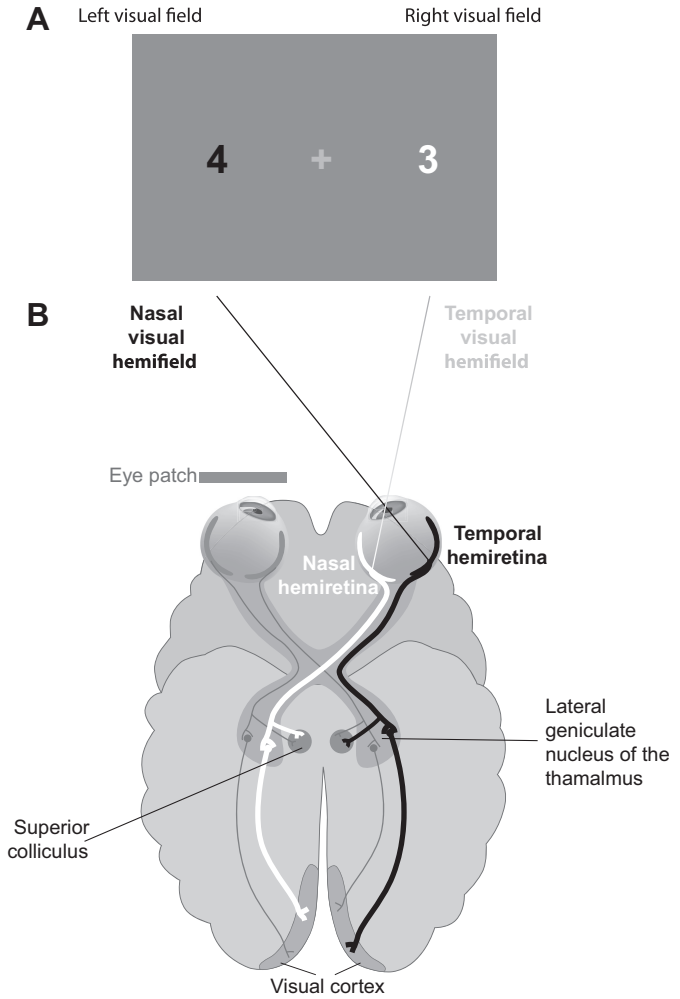

Fig. 1. *A*: example trial. In each trial, two colored digits were displayed at 7° to either side of the fixation cross on a black background. One of the two colors was designated as the target color. *B*: effect of the eye-patching procedure on the retinal representation of target and distractor stimuli. When the left eye is occluded, the digit to the right appears in the temporal visual field (and is projected onto the nasal hemiretina). The digit to the left appears in the nasal visual field and is represented on the temporal hemiretina. [Copyright 2011 by Alila07, Dreamstime.com, adapted with permission.]

onset and is generated in extrastriate areas of the ventral visual processing stream (Hopf et al. 2000). Numerous studies have demonstrated that the N2pc is generated during the rapid attentional selection of candidate target objects among distractors in visual search (e.g., Luck and Hillyard 1994a, 1994b; Eimer 1996; Woodman and Luck 1999; Eimer and Grubert 2014) and also by target-matching but task-irrelevant visual events that capture attention (e.g., Eimer and Kiss 2008; Lien et al. 2008). Because the N2pc is elicited by attended visual stimuli in perceptually balanced bilateral stimulus displays, it is not caused by sensory asymmetries between visual hemifields but is a genuine reflection of spatially selective attentional processing.

In the present study, we measured the N2pc component as a marker of the spatial selection of target objects in the temporal or nasal visual field. Our participants reported the identity of a color-defined target digit that was presented to the left or right of fixation together with a task-irrelevant distractor stimulus in the opposite visual field (see Fig. 1*A*). In this task, target stimuli have previously been shown to elicit robust N2pc components (Grubert and Eimer 2013). To discern N2pc components to targets presented in the temporal versus nasal field, in different blocks, participants performed the task with their left or right eye patched or without any eye patching (full visual field condition). In the absence of eye patching, target and distractor stimuli both projected to the nasal and temporal hemiretinae. In contrast, when one eye was patched, target and distractor projected to separate hemiretinae (see Fig. 1*B*). When the right eye was open (and the left eye was patched), stimuli on the left side appeared in the nasal hemifield and projected to the temporal hemiretina, whereas stimuli on the right appeared in the temporal hemifield and projected to the nasal hemiretina. These spatial relationships were reversed when the left eye was open and the right eye was patched. Because the N2pc is an established ERP marker of spatially selective attentional target processing (Luck and Hillyard 1994a, 1994b; Eimer 1996), an attentional advantage for target stimuli in the temporal visual hemifield should be reflected by larger and/or earlier N2pc components for temporal compared with nasal targets.

EXPERIMENT 1

Methods

Participants. Thirteen paid volunteers participated. One participant was excluded because of excessive blinks and eye movements. The mean age of the 12 remaining participants was 32.8 yr, ranging from 24 to 46 yr. There were six female and six male participants. One participant was left handed. Written informed consent was obtained from the participants before the experiment, which was approved by the Psychology Ethics Committee of Birkbeck College. All participants had normal or corrected to normal vision and color vision.

Stimuli and procedures. Stimuli were presented on a 22-inch LCD monitor with 5-ms RT at a resolution of 1,280 × 1,024 pixels and a 100-Hz refresh rate. Stimulus presentation and response collection were controlled by a PC running under Windows XP using Matlab (Mathworks) and the Cogent 2000 and Cogent Graphics toolboxes (Cogent 2000 team and John Romaya, University College London, London, UK). Participants viewed the screen from a distance of ~80 cm.

Stimuli were presented for 150 ms against a black background. A central gray fixation cross was presented throughout each trial. Each search array contained two colored digits extending vertically over 1° of visual angle. The two digits were presented to the left and right of fixation at a horizontal eccentricity of 7° (see Fig. 1*A*). Digit identities (1, 2, 3, and 4) were chosen randomly across trials, with the constraint that there were always two different digits on each trial. Digit colors were red (CIE color coordinates 0.628/0.340), green (0.268/0.566), blue (0.182/0.181), and yellow (0.418/0.474). All colors were equiluminant (8.8 cd/m^2). Each of the four colors was assigned to be the target color for three participants, and the remaining three colors served as distractor colors. In each trial, one of the digits had the target color and the other digit had one of the distractor colors. Distractor colors as well as target sides (left or right of fixation) were balanced within each block and occurred in random order.

The experiment included three blocked viewing conditions. In the no patch condition, participants viewed the screen with

both eyes. The left or right eye was patched in the left eye patched and right eye patched conditions, respectively. On the basis of these viewing conditions, three types of visual field conditions were computed (see Fig. 1*B*). The full visual field (full retina) condition was obtained in no patch blocks. To obtain ERPs for trials with targets in the nasal visual hemifield (projecting on the temporal hemiretina), data from trials where targets appeared on the left side in left eye patched blocks and from trials with right targets in right eye patched blocks were combined. ERPs for trials with targets in the temporal visual hemifield (projecting on the nasal hemiretina) were obtained by combining data from trials where targets appeared on the right side in left eye patched blocks and from trials with left targets in right eye patched blocks. Participants performed three successive blocks of 66 trials in each viewing condition (no patch, left eye patched, and right eye patched), resulting in an equal number of trials in each visual field condition (full visual field, temporal target, and nasal target). The sequence of viewing conditions was counterbalanced across participants.

Trials were separated by an interval of 1,650 ms. The participants' task was to identify the target-color digit (1, 2, 3, or 4) on each trial and to report its identity by pressing one of four horizontally aligned response keys with their left or right index or middle finger. Target identity and response keys were spatially compatible, with the leftmost key assigned to the digit "1" and the rightmost key to the digit "4." Participants were instructed to answer as fast and accurately as possible and to maintain fixation throughout the experiment. One practice block for the viewing condition with which the respective participant started the experiment was conducted before the first experimental block.

Electroencephalographic data recording and analysis. A continuous electroencephalogram (EEG) was DC recorded from 64 electrodes placed in an elastic cap according to the standard 10/10-electrode system. The EEG was sampled at a rate of 500 Hz and digitally low-pass filtered with 40 Hz. No further filters were applied after data acquisition. All electrodes were online referenced to the left earlobe and offline rereferenced to the average of both earlobes. Trials were segmented from 100 ms before to 600 ms after the stimulus onset, and ERPs were computed relative to a 100-ms prestimulus baseline. Trials including eye movements [± 30 μV at the bipolar horizontal electrooculogram (HEOG) channel] or blinks (± 60 μV at Fp1/2) were removed from further analysis. For trials including muscular artifacts (± 80 μV at all other electrode sites), only the signal in the affected electrodes was removed. Trials including response errors, missing, anticipatory (faster than 200 ms), or very slow (slower than 1,500 ms) responses were also excluded. The EEG was averaged for each combination of viewing condition (no patch, left eye patched, and right eye patched) and side of target digit (left or right). In a second step, the EEG was further averaged with respect to the visual hemifield in which the target stimulus appeared. Left eye patched trials with left side targets and right eye patched trials with right side targets were averaged to measure ERPs to targets in the nasal visual hemifield. Left eye patched trials with right side targets and right eye patched trials with left side targets were averaged to obtain ERPs for targets in the temporal visual hemifield. No patch trials constituted the full visual field condition.

N2pc components to targets were quantified on the basis of mean amplitudes in a 190- to 280-ms poststimulus time window at lateral posterior electrode sites PO7 and PO8. These lateral posterior electrode sites are the standard positions for measuring N2pc components, because N2pc amplitudes are typically largest at these sites (e.g., Eimer and Grubert 2013, 2014). N2pc onset latencies were determined on the basis of difference waveforms (subtracting ERPs ipsilateral to the target from contralateral ERPs). Subsamples of grand-averaged difference waves were computed in which always one participant in turn was excluded from the subsample scores to obtain jack-knifed difference waves (Miller et al. 1998). N2pc onset latencies were determined as the point in time at which an absolute threshold of -0.5 μV in each waveform was reached. Onset latency differences were assessed by means of repeated-measures ANOVA and follow-up *t*-tests, for which *F*- and *t*-values were corrected according to formulas previously described by Miller et al. (1998) and Ulrich and Miller (2001). All *t*-tests were two-tailed and Bonferroni corrected where necessary. Greenhouse-Geisser corrected *P* values are reported for effects that violate the assumption of sphericity.

Since deviations of gaze from fixation could have contributed to, or even caused, nasotemporal asymmetries, we did not only use the HEOG as an indicator of eye movements for artifact rejection but statistically analyzed the residual HEOG of all trials that were included in the ERP analysis by comparing HEOG waveforms recorded ipsilateral and contralateral to the target. A larger negativity for the contralateral HEOG indicates minor residual deviations of gaze toward the location of the target, and a HEOG difference of 15 μV corresponds to a gaze deviation of $\sim 1°$ (Lins et al. 1993).

Results

Behavioral results. Trials faster than 200 ms or slower than 1,500 ms (0.1% of all trials) and trials with incorrect responses (2.9% of all trials) were excluded from the analysis. RTs were subjected to repeated-measures ANOVA with the variable visual field of target (full visual field, target in temporal hemifield, and target in nasal hemifield), which revealed a main effect [$F(2,22) = 11.62$, $P < 0.001$]. Followup *t*-tests showed that participants responded faster in the full visual field condition without eye patching (546 ms) relative to blocks where one eye was patched and the target appeared either in the temporal [568 ms, $t(11) = 3.53$, $P = 0.01$] or nasal visual hemifield [565 ms, $t(11) = 4.08$, $P < 0.01$]. RTs between the two hemifield conditions (nasal vs. temporal target) did not differ [$t(11) < 1.00$].

Mean error rates were generally low in all three visual field conditions (full visual field: 2.3%, nasal target: 3.2%, and temporal target: 2.9%), and there was no effect of visual field on error rates [$F(2,22) < 1.00$].

ERP results. N2PC. Figure 2*A* shows grand-averaged ERPs measured at electrode sites PO7/8 contralateral and ipsilateral to the target stimulus separately for the three visual field conditions (full visual field, target in temporal hemifield, and target in nasal hemifield). A solid N2pc was triggered in all three conditions. However, and unexpectedly, the N2pc to targets in the temporal hemifield was smaller relative to the N2pc for targets in the nasal hemifield and the target N2pc measured in the full visual field condition. This can also be seen in the N2pc difference waves shown in Fig. 2*B*, which

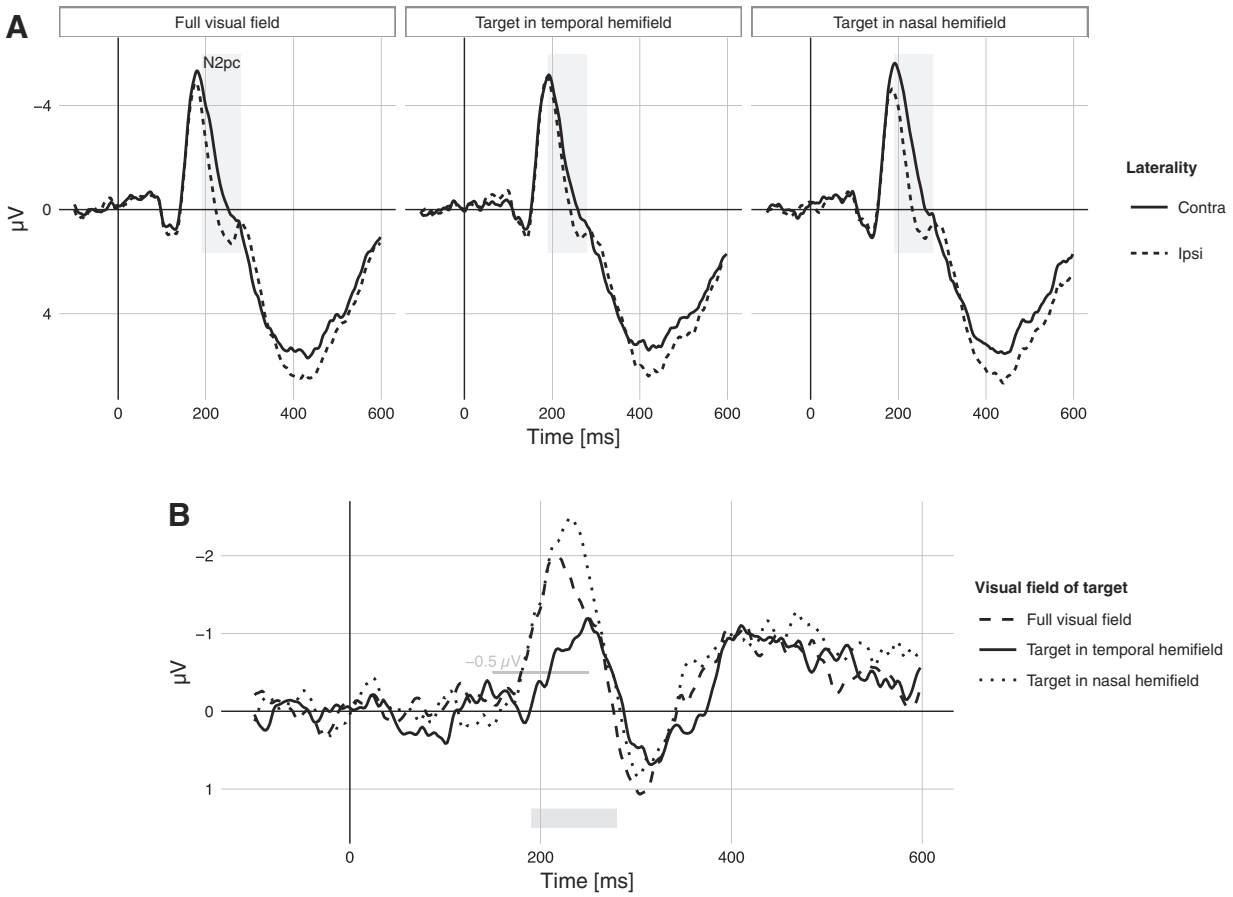

Fig. 2. *A*: contralateral and ipsilateral event-related potentials (ERPs) at electrodes PO7 and PO8 for all three visual field conditions (full visual field, target in the nasal hemifield, and target in the temporal hemifield). Shaded areas indicate the N2pc measurement interval (190- to 280-ms poststimulus). *B*L contralateral-ipsilateral difference waves of electrodes PO7 and PO8 for the same three visual field conditions. The gray line at the center indicates the fixed threshold of -0.5 μV used to determine the onset latency of the N2pc. The gray bar at the bottom indicates the time window across which amplitude statistics were computed.

were obtained by subtracting ipsilateral from contralateral ERPs separately for each visual field condition. The N2pc to targets in the temporal hemifield was attenuated and delayed relative to the N2pc to targets in the nasal hemifield and to the target N2pc in the full visual field condition. The N2pc to nasal-hemifield targets and to targets in the full field condition emerged at the same time, and the amplitude of the nasal N2pc was numerically larger than the full visual field N2pc.

This pattern of N2pc results was statistically confirmed by repeated-measures ANOVA with the factors visual field of target (full visual field, temporal target, and nasal target) and laterality (electrode contralateral vs. ipsilateral to the target) carried out on mean amplitudes measured in the 190- to 280-ms poststimulus time window. A main effect of laterality [$F(1,11) = 24.18$, $P < 0.001$], reflecting the presence of reliable N2pc components, was accompanied by a visual field × laterality interaction [$F(2,22) = 8.05$, $P < 0.01$], indicating that N2pc components differed across the three visual field conditions. Bonferroni-corrected post hoc *t*-tests confirmed that the N2pc to temporal hemifield targets was attenuated relative to the N2pc triggered by nasal targets [$t(11) = 3.62$, $P < 0.01$]. There were no reliable N2pc amplitude differences (after Bonferroni correction) between the target N2pc in full visual field blocks and the N2pc to targets in the temporal hemifield [$t(11) = 2.14$, $P = 0.16$] or nasal hemifield [$t(11) = 2.18$, $P = 0.17$]. To find out whether there were additional earlier nasotemporal differences at lateral posterior electrodes (in particular modulations of the visual evoked P1 component), additional moving-window ANOVAs (averaging window: 50 ms, step width: 5 ms) with the factor target type (nasal or temporal) were conducted across the whole poststimulus interval, starting from the stimulus onset. These analyses confirmed that there were no significant nasotemporal asymmetries at lateral posterior electrodes PO7/8 contralateral or ipsilateral to the target at any point before the onset of the N2pc.

To assess N2pc onset latency differences between full field, nasal, and temporal targets, jack-knife-based N2pc onset latency estimates were subjected to repeated-measures ANOVA, which revealed a main effect of visual field of target [$F_c(2,22) = 8.94$, $P < 0.01$]. Followup *t*-tests confirmed that the N2pc to targets in the temporal hemifield (210 ms) was indeed delayed relative to the N2pc to nasal-hemifield targets [181 ms, $t_c(11) = 3.16$, $P = 0.03$] and relative to the target N2pc in the full visual field condition [181 ms, $t_c(11) = 3.58$, $P = 0.01$]. There was no N2pc onset latency difference between nasal-hemifield targets and targets in full visual field blocks [$t_c(11) < 1.00$].

HEOG. Figure 3, *left*, shows difference waves obtained by subtracting the grand-averaged HEOG recorded on the side ipsilateral to the target from the contralateral HEOG separately for temporal, nasal, or full visual field targets in *experiment 1*.

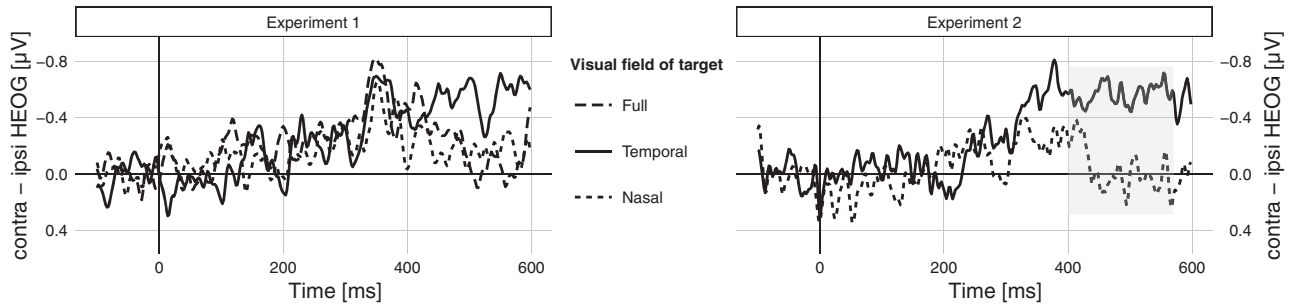

Fig. 3. Horizontal electrooculogram (HEOG) difference waves in *experiment 1* (*left*) and *experiment 2* (*right*, target-distractor trials only). Negative deflections indicate eye movements toward the target. The gray area on the *right* indicates the period of the significant laterality (contralateral vs. ipsilateral) × visual field (temporal vs. nasal) interaction.

In these difference waveforms, a tendency to move the eyes toward the side of the target will be reflected by negative (upward-going) values. As can be seen from these HEOG waveforms, residual eye movements toward the target were minimal [below 1 μV, where a value of 15 μV would reflect a gaze shift of 1° (Lins et al. 1993)] and did not differ systematically between temporal, nasal, and full visual field targets. This was confirmed by a set of moving-window repeated-measures ANOVAs (averaging window: 50 ms, step width: 5 ms) conducted across the whole 600-ms poststimulus interval with the variables visual field (full, temporal target, and nasal target) and HEOG side (contralateral vs. ipsilateral to target), which did not reveal a significant interaction between these two factors for any time window.

NONLATERALIZED VISUAL ERP COMPONENTS. Figure 4 shows ERPs at lateral posterior electrodes (averaged across PO7 and PO8) in binocular full visual field blocks (solid line) and in monocular blocks where one eye was patched (dashed line, collapsed across left eye patch and right eye patch blocks). Both P1 and N1 components were delayed under monocular compared with binocular viewing conditions. This was confirmed by *t*-tests of P1 and N1 peak latencies (obtained within 80- to 160-ms and 150- to 250-ms poststimulus time windows, respectively). Both P1 (138 vs. 117 ms) as well as N1 (190 vs. 180 ms) components peaked earlier in binocular compared with monocular blocks [both $t\,(11) > 4.1$, both $P < 0.002$], in line with the observation that RTs were faster in binocular blocks (see above).

Discussion

The N2pc revealed an attentional nasotemporal asymmetry. However, the direction of this asymmetry was the opposite of our predictions. We assumed that a temporal hemifield advantage would lead to a larger and earlier N2pc for targets in the temporal hemifield compared with targets in the nasal visual hemifield. Results revealed the reverse pattern, namely, a reduced and delayed N2pc for targets in the temporal hemifield compared with targets in the nasal visual hemifield. The analysis of contralateral and ipsilateral HEOG demonstrated that there were no systematic differences in eye gaze across the different visual field conditions, thereby ruling out the possibility that the unexpected direction of the nasotemporal asymmetry on N2pc components was linked to small eye movements that went undetected by our artifact rejection procedures.

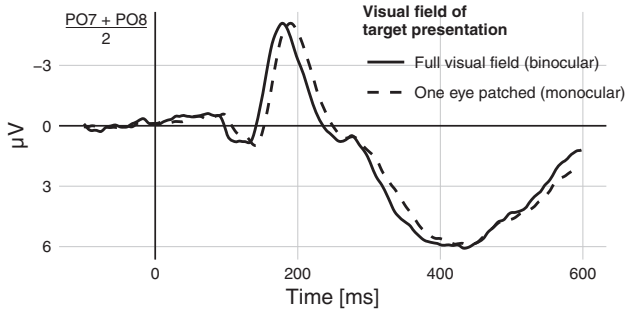

Fig. 4. Grand-averaged ERP waveforms at lateral posterior electrodes (PO7/8) in the full view condition and in blocks where one eye was patched (collapsed across blocks with left eye and right eye patching). P1 and N1 components were delayed under monocular viewing conditions relative to full view blocks.

Another notable finding of *experiment 1* was the delay of early visual P1 and N1 components under monocular relative to binocular viewing conditions (Fig. 4), which suggests that early perceptual stages in extrastriate visual areas are systematically delayed under conditions where one eye is patched. In line with these results, RTs were slower in these conditions relative to the full visual field condition. This RT delay may be partially caused by a difference in the sensory processing of monocular stimuli. Although a monocular stimulus finally reaches the same neural activation level as a binocular stimulus, the ERP results suggest that it takes ~10–20 ms longer until this activation level is reached. The observed RT difference between monocular and binocular viewing conditions (19 ms) corresponds to these latency differences in the processing of binocular and monocular stimuli at early sensory-perceptual stages. It should be noted that even though the N2pc to temporal targets was delayed relative to the target N2pc in full view blocks, there was no N2pc onset latency difference between nasal and full view targets, suggesting that the selective attentional processing of targets versus distractors was not uniformly delayed under monocular compared with binocular viewing conditions.

To account for the reduced amplitude and delayed onset of the N2pc to temporal versus nasal targets observed in *experiment 1*, it is important to note that targets were not presented in isolation but were always accompanied by distractors at the opposite side (see also Rafal et al. 1989; Jóhannesson et al. 2012). It has previously been shown that the interference produced by temporal distractors is stronger than that of nasal distractors (Rafal et al. 1989; Walker et al. 2000). If a distractor in the temporal visual field has a greater potential to interfere with the processing of a target object on the opposite side relative to a nasal distractor, the successful attentional selection of a target may require a

greater degree of inhibition of temporal compared with nasal distractors. Distractor inhibition might have affected the N2pc, because previous research has shown that when a target and a distractor are simultaneously presented on opposite sides, the N2pc component reflects not only an enhanced negativity contralateral to the target but also an additional positive deflection (P_D component) contralateral to the distractor that has been associated with distractor inhibition (Hickey et al. 2008). If the N2pc reflects the additive contributions of both target selection and distractor inhibition, the N2pc results of *experiment 1* could be primarily driven by a nasotemporal asymmetry in distractor inhibition processes. Stronger interference from a temporal distractor would elicit increased inhibition, as indicated by an increased P_D. This would result in an increased overall N2pc to a nasal target that is accompanied by a temporal distractor relative to trials where a temporal target is accompanied by a nasal distractor.

EXPERIMENT 2

Experiment 2 was designed to directly test the hypothesis that temporal distractors trigger a larger inhibition-related P_D component than nasal distractors. This experiment included distractor-only displays, which contained two distractor digits in two different nontarget colors at the same two locations at which a target and a distractor appeared in target-distractor trials. When distractor-only displays were viewed with one eye patched, one of the two distractor objects was located in the temporal and the other in the nasal visual field. Electrodes contralateral to a temporal distractor were per definition ipsilateral to a nasal distractor, and electrodes ipsilateral to a temporal distractor were contralateral to a nasal distractor. Comparing posterior lateral electrodes contralateral and ipsilateral to a temporal distractor in distractor-only trials therefore enabled us to determine whether a temporal distractor led to a more pronounced P_D relative to a nasal distractor. Distractor-only trials were randomly interspersed with target-distractor trials. Based on the results of *experiment 1*, we expected that the N2pc to temporal targets would be smaller than the N2pc to nasal targets. If the P_D to a temporal distractor in distractor-only trials occurred in the same time window as the difference between the temporal and nasal N2pc in target-distractor trials, this would provide an explanation for the more pronounced N2pc to nasal compared with temporal targets.

Methods

Participants. Eight paid participants (5 female participants and 3 male participants; 2 left handed) performed *experiment 2* after giving written informed consent. Their mean age was 32 yr, ranging from 26 to 40 yr. All of them had normal or corrected to normal vision and color vision. *Experiment 2* was also approved by the Psychology Ethics Committee of Birkbeck College.

Stimuli and procedures. The stimuli, apparatus, and procedures were described above in *experiment 1* with two exceptions. In *experiment 2*, there were five consecutive left eye patched and five consecutive right eye patched blocks and no unpatched (full visual field) blocks. The crucial difference between *experiments 1* and *2* was the introduction of distractor-only trials. Distractor-only trials did not contain a target-color digit but instead two digits in two randomly selected nontarget colors. The participants' task was to report the value of the color-defined target digit in target-distractor trials and to refrain from responding in distractor-only trials. Each of the five left eye patched and five right eye patched blocks included 48 target-distractor and 24 distractor-only trials, randomly intermixed. The order of viewing conditions (left eye patched vs. right eye patched) was balanced across participants.

EEG data recording and analysis. EEG data recording and processing as well as the computation of N2pc waveforms for temporal and nasal targets on target-distractor trials were identical to *experiment 1*. For distractor-only trials, electrode laterality was defined with respect to the location of a distractor in the temporal visual field. In blocks where the right eye was patched, PO8 was defined as contralateral electrode and PO7 as the ipsilateral electrode. In blocks where the left eye was patched, these labels were reversed. In the combined ERP waveforms for distractor-only trials, electrode laterality (contralateral vs. ipsilateral) was therefore always defined relative to the temporal distractor item. As in *experiment 1*, N2pc onset latency estimates were determined with the jack-knife procedure by Miller et al. (1998; see also Ulrich and Miller 2001), using the same fixed threshold of 0.5 μV.

Results

Behavioral results. Trials with incorrect responses (4.6% of all trials) and trials with responses faster than 200 ms or slower than 1,500 ms (<0.02% of all trials) were excluded from the analysis. A paired *t*-test indicated no significant difference between responses to temporal (620 ms) versus nasal targets [626 ms, $t(7) < 1.00$]. There was also no significant effect of target location on error rates [temporal target: 3.1%, nasal target: 4.9%, and distractor only: 5.7%, $F(2,14) = 2.05$, $P = 0.17$].

ERP results. N2PC. As shown in Fig. 5*A*, targets in the temporal and nasal visual hemifield both elicited N2pc components. As in *experiment 1*, the N2pc was larger for targets in the nasal compared with temporal visual field. Repeated-measures ANOVA with the variables visual field (target in the temporal hemifield and target in the nasal hemifield) and laterality (electrode contralateral vs. ipsilateral to the target) on ERP mean amplitudes measured at PO7/8 in the 190- to 280-ms poststimulus time window confirmed that temporal and nasal targets triggered an N2pc [main effect of laterality, $F(1,7) = 14.75$, $P < 0.01$] and that the N2pc component was larger for nasal compared with temporal targets [visual field × laterality interaction, $F(1,7) = 9.97$, $P = 0.02$]. As shown in the contralateral-ipsilateral N2pc difference waves in Fig. 5*B*, the N2pc to temporal targets was not only attenuated but also numerically delayed relative to the N2pc to nasal targets (204 vs. 184 ms), similar to the N2pc latency shift observed in *experiment 1*. However, here the latency difference was not statistically significant [$t_c(7) < 1.00$].

Critically, as predicted by our distractor inhibition account for the nasotemporal asymmetry, an enhanced positivity (P_D component) was elicited on distractor-only trials contralateral to temporal distractors (Fig. 5*A*, *right*). This P_D can be seen more clearly in the difference waveform obtained by subtracting distractor-only ERPs measured at electrodes ipsilateral to the temporal distractor from contralateral ERPs (Fig. 5*B*, dashed line). Although small in size, this P_D component was

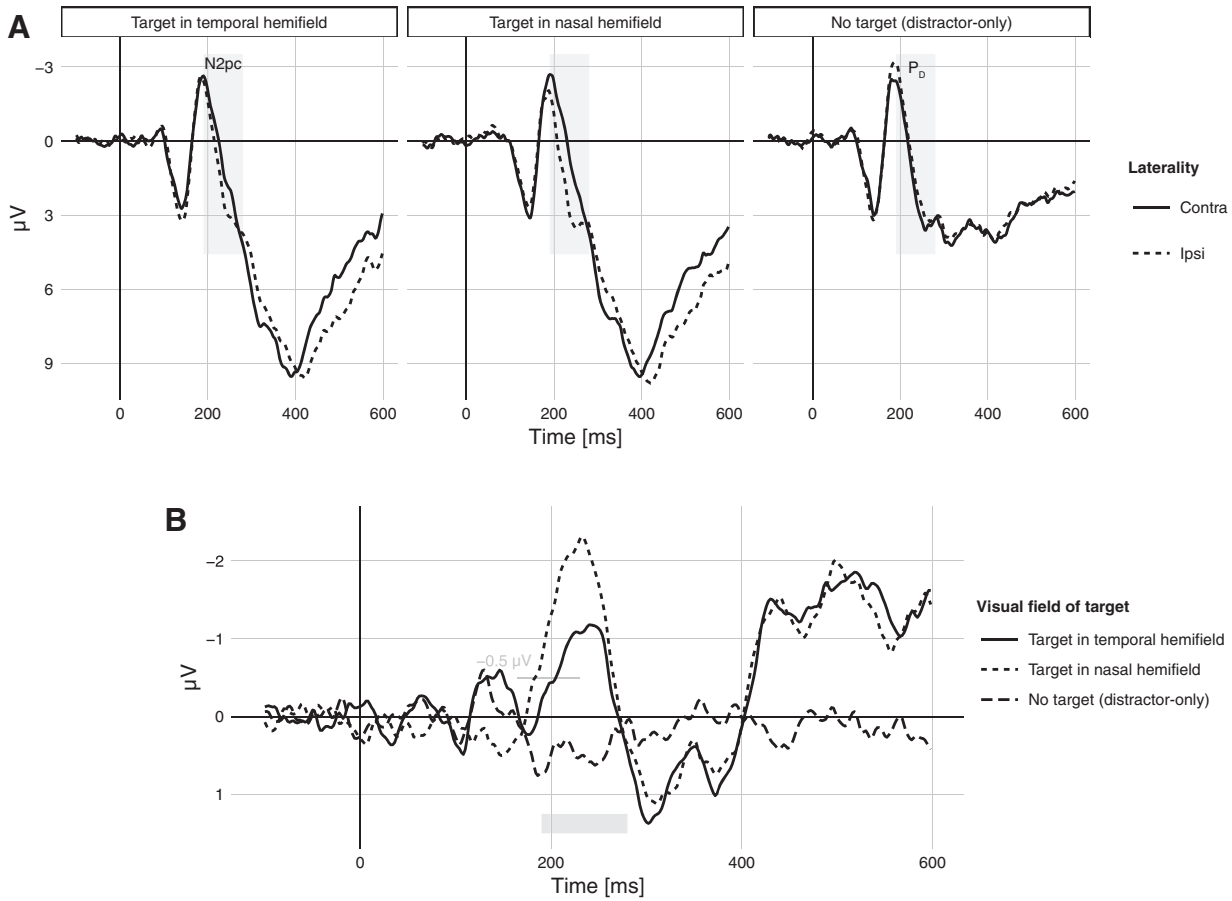

Fig. 5. *A*: contralateral and ipsilateral ERP waveforms at PO7/8 for target-distractor trials with a temporal or a nasal target and for distractor-only trials. For the temporal and nasal conditions, contralateral and ipsilateral electrode location are defined relative to the location of the target in the left or right visual field. For distractor-only trials, laterality is defined relative to the location of a temporal distractor. The gray area indicates the N2pc measurement time window (190- to 280-ms poststimulus). *B*: contralateral minus ipsilateral difference waveforms for trials with a target in the temporal or nasal hemifield and distractor-only trials. For distractor-only trials, ERPs at PO7/8 ipsilateral to a temporal distractor were subtracted from contralateral ERPs, resulting in a contralateral positivity (P_D component) in the N2pc time window. The short gray line at -0.5μV indicates the threshold used for the onset latency analysis. The gray bar at the bottom indicates the time window used to compute amplitude statistics.

present during the same time interval as the target N2pc. A paired *t*-test comparing ERP mean amplitudes at electrodes contralateral and ipsilateral to the temporal distractor on distractor-only trials during the N2pc time window (190- to 280-ms poststimulus) confirmed that the P_D component was statistically reliable [$t(7) = 2.51$, $P = 0.04$]. As in *experiment 1*, ERPs to target-distractor displays were analyzed across the whole poststimulus interval with moving-window ANOVAs (averaging window: 50 ms, step width: 5 ms) with the factor target type (nasal or temporal) to identify any additional early nasotemporal differences at lateral posterior electrodes. No reliable nasotemporal asymmetries were present before the onset of the N2pc.

HEOG. Figure 3, *right*, shows difference waves obtained by subtracting the grand-averaged ipsilateral HEOG from the HEOG recorded contralateral to the target separately for temporal and nasal targets in *experiment 2*. A tendency to move the eyes toward the side of the target is reflected by negative values. As in *experiment 1*, residual eye movements toward the target were minimal (below 1 μV). A set of moving-window repeated-measures ANOVAs (averaging window: 50 ms, step width: 5 ms) conducted across the 600-ms poststimulus interval with the variables visual field (temporal vs. nasal target) and HEOG side (contralateral vs. ipsilateral to target) revealed no difference during the first 400 ms after the stimulus onset. Between 400- and 570-ms poststimulus, HEOG deviations were larger for temporal targets ($P < 0.05$), indicative of a small residual tendency for eye movements toward the side of a temporal target during this late time interval (note that visual stimuli were shown for 150 ms and were therefore no longer present during this interval).

Discussion

Experiment 2 replicated the main result of *experiment 1* that N2pc components are reduced in size in response to target objects in the temporal visual field relative to nasal targets. The absence of any systematic HEOG differences between trials with temporal and nasal targets during the first 400 ms after the stimulus onset again confirms that this differential N2pc modulation was not caused by undetected eye movements. Importantly, the analysis of distractor-only trials provided support for our hypothesis that this nasotemporal N2pc asymmetry is linked to differences in the amount of inhibition triggered by temporal versus nasal distractors. In distractor-only trials, where a distractor object in the temporal visual field was presented together with a different distractor in the nasal

hemifield, a reliable net positivity in the N2pc time window was observed contralateral to the temporal distractors. This observation is in line with the assumption that temporal distractors trigger an increased amount of attentional inhibition relative to nasal distractors and, therefore, larger contralateral P_D components. This suggests that the larger P_D to temporal distractors enhances the overall N2pc amplitude on trials with nasal targets and temporal distractors relative to trials where a temporal target is accompanied by a nasal distractor, thus contributing to the nasotemporal N2pc asymmetry observed on target-distractor trials in both experiments. Note that the P_D component on distractor-only trials only reflects the relative difference in the amount of attentional inhibition triggered by temporal and nasal distractors under conditions where no target is simultaneously present rather than the absolute amount of inhibition elicited by each of these distractors when they are presented together with a target object on the opposite side. This may account for the fact that the absolute nasotemporal N2pc asymmetry observed on target-distractor trials was considerably larger than the nasotemporal P_D asymmetry measured on distractor-only trials (see Fig. 5*B*).

The topographical maps shown in Fig. 6 show the scalp distribution of the P_D component measured in distractor-only trials of *experiment 2* together with the topography of the target N2pc component obtained under full view conditions in *experiment 1*. Both maps were computed by subtracting ERP mean amplitudes measured in the N2pc time window (190- to 280-ms poststimulus) ipsilateral to a temporal distractor (for the P_D component) or ipsilateral to a target (for the N2pc component) from ERP mean amplitudes at corresponding contralateral electrodes and mirroring the resulting difference amplitudes to obtain symmetrical voltages for both hemispheres. Even though the P_D component was considerably smaller than the N2pc (note the different voltage scales on the two maps), the topography of these two components was similar, in line with previous observations that P_D and N2pc components overlap in terms of their scalp distributions (Hickey et al. 2008).

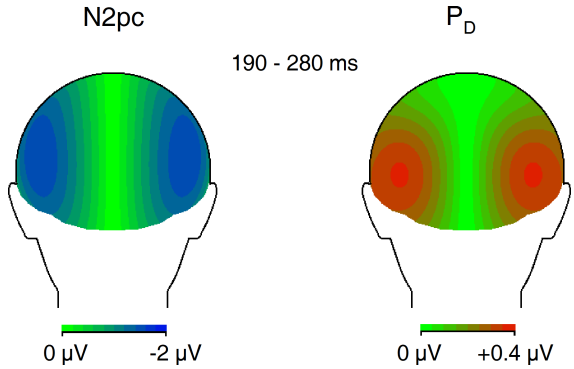

Fig. 6. Topographical maps of the N2pc component measured in the full visual field condition of *experiment 1* (*left*) and the P_D component obtained for distractor-only trials in *experiment 2* (*right*). Both maps were constructed by subtracting ipsilateral from contralateral ERPs and mirroring the resulting difference waveforms to obtain symmetrical voltages over both hemispheres (see text for details). The N2pc map shows a contralateral negativity over posterior electrode sites, and the P_D map shows an effect with opposite polarity (a contralateral positivity) but a similar topography. Note the different voltage scales for the N2pc and P_D maps. Each isocontour line represents a change of 0.25 μV for the N2pc map and 0.05 μV for the P_D map.

GENERAL DISCUSSION

To investigate whether the nasotemporal asymmetry observed in previous behavioral experiments is generated at the stage of attentional target selection, we used an eye-patching procedure and measured N2pc components to targets in the temporal or nasal visual hemifield. The results of this study provide novel ERP evidence for the existence of a genuinely attentional nasotemporal asymmetry. However, the direction of this asymmetry was unexpected. Based on a behavioral temporal hemifield advantage (e.g., Rafal et al. 1991), we expected to find a more pronounced N2pc to targets in the temporal compared with the nasal hemifield. However, *experiment 1* showed that the N2pc to temporal targets was in fact reduced in size compared with nasal targets. This finding was replicated in *experiment 2*. There were no lateral posterior nasotemporal asymmetries for ERP components before the N2pc. This strongly suggests that nasotemporal N2pc asymmetries do not reflect a general enhancement of contralateral visual components to stimuli in the nasal hemifield, as such a low-level visual bias toward nasal stimuli should have been most pronounced for short-latency visual evoked responses such as the exogenous P1 component.

Experiment 2 provided a possible explanation for this surprising pattern of N2pc results. The analyses of lateralized ERP components on distractor-only trials with one nasal and one temporal distractor object demonstrated that temporal distractors elicited a larger contralateral positivity than nasal distractors in the N2pc time window. As a contralateral positivity to distractor objects (or P_D component) has previously been associated with attentional inhibition (Hickey et al. 2008), this result suggests that temporal distractors are inhibited more strongly than nasal distractors. This nasotemporal asymmetry in distractor inhibition, as reflected by the P_D component, could be responsible for the fact that overall N2pc amplitudes are larger on trials with temporal distractors and nasal targets relative to trials with nasal distractors and temporal targets. Because the N2pc reflects overall amplitude differences between posterior electrodes contralateral and ipsilateral to a target, an enhanced positivity contralateral to a temporal distractor (i.e., a larger P_D component) that accompanies the selection-related enhanced negativity contralateral to a nasal target will increase the overall contralateral-ipsilateral difference on these trials relative to trials with a nasal distractor and a temporal target, where the P_D component is less pronounced.

Distractors in the temporal hemifield may require attentional inhibition, resulting in larger P_D components, because they are generally more likely to capture attention than nasal distractors. Our results therefore suggest that instead of being an attentional advantage for targets in the temporal hemifield, nasotemporal asymmetries may be better conceived of as an increased capacity of temporal distractors to capture attention, which needs to be counteracted by top-down inhibition under conditions where a nasal target and a temporal distractor compete for attentional selection. This account of nasotemporal asymmetries in distractor interference is in line with the observation of Walker et al. (2000) that temporal distractors interfered more than nasal distractors, as reflected by slower saccade latencies on trials with temporal distractors. The fact that this effect was found for a control group and not for hemianopic participants led Walker et al. to conclude that this

nasotemporal asymmetry is mediated by cortical areas. The experimental design of Walker et al. also involved target-only trials where a single target stimulus was present in either the temporal or the nasal visual hemifield. In the absence of distractors, saccade latencies toward temporal and nasal targets did not differ, suggesting an important role of distractors for nasotemporal asymmetries. In a study similar to Walker et al. (2000), Rafal et al. (1990) also found increased distractor interference effects on saccade latencies produced by temporal compared with nasal distractors, but only for hemianopic participants and not for healthy control subjects, indicative of an involvement of subcortical pathways in nasotemporal asymmetries. Regardless of the neural locus of these asymmetries, the important fact is that both Rafal et al. (1990) and Walker et al. (2000) found evidence for increased distractor interference for distractors in the temporal compared with the nasal visual field, which is in line with our suggestion that temporal distractors are more likely to capture attention, unless they are subject to top-down inhibition.

In contrast to the marked nasotemporal asymmetries that were found for N2pc and P_D components in the present study, there were no behavioral differences between trials with temporal targets/nasal distractors and trials with nasal targets/temporal distractors. If temporal distractors are successfully inhibited, as reflected by the presence of P_D components to these distractors, one may expect them to interfere less on trials where nasal targets have to be selected, thus resulting in better performance on these trials. However, this argument assumes that inhibition is selectively applied exclusively to temporal distractors and not to nasal distractors, which is unlikely to be the case. In *experiment 2*, P_D components on distractor-only trials were computed on the basis of relative ERP differences between the hemisphere contralateral and ipsilateral to a temporal distractor that was accompanied by another distractor on the opposite (nasal) side. The P_D component therefore reflects the relative difference in top-down inhibition that was applied to a temporal versus nasal distractor rather than the absolute amount of inhibition associated with a temporal distractor. The degree of inhibition applied to temporal versus nasal distractors may be a function of their respective capacity to capture attention. In other words, temporal distractors are inhibited more strongly than nasal distractors because of their greater potential to attract attention. If this is the case, the absence of behavioral differences between trials with temporal and nasal distractors reflects the fact that the larger inhibition applied to temporal distractors was sufficient to counteract their greater ability to produce behavioral interference effects.

While this hypothesis that top-down inhibition is applied differentially to distractors in the temporal versus nasal visual field must remain speculative at present, it might account for some of the discrepancies in the literature on behavioral nasotemporal asymmetries. For example, the presence of temporal distractor interference effects for hemianopic participants and the absence of such effects for a control group reported by Rafal et al. (1990) and the exactly opposite pattern of between-group differences found by Walker et al. (2000) might be related to systematic differences in the relative amount of inhibition applied to temporal versus nasal distractors in these two studies. Future studies on nasotemporal asymmetries in patients and control participants would definitely benefit from the combination of behavioral and electrophysiological measures of target selection, distractor interference, and distractor inhibition, as the presence of such asymmetries might be reflected by some of these measures but not by others.

In addition to suggesting that temporal hemifield advantages are linked to an increased suppression of temporal compared with nasal distractors and may therefore not be directly linked to benefits on the attentional processing of temporal target stimuli, our finding that nasotemporal asymmetries can be observed for cortical ERP components such as the N2pc and P_D strongly suggests that these asymmetries are present at cortical levels of visual processing (cf. Bompas et al. 2008; Walker et al. 2000). Bompas et al. (2008) arrived at a similar conclusion. These authors used S cone stimuli that are invisible to the retinotectal pathway and replicated the original finding of preferential orienting toward stimuli in the temporal hemifield (Posner and Cohen 1980). This demonstrates that nasotemporal asymmetries do not necessarily rely on the retinotectal pathway but might also be mediated by the geniculostriate pathway or higher cortical regions (Bompas et al. 2008). Although these findings suggest a cortical contribution to nasotemporal asymmetries, they do not rule out a subcortical basis. Neuroanatomic studies have provided evidence that the visual pathway carries stronger projections from the nasal relative to the temporal hemiretinae (Perry et al. 1984; Williams et al. 1995). A nasotemporal asymmetry has been reported for the retinotectal pathway (Perry and Cowey 1984) and for projections to the LGN (Perry et al. 1984). A nasotemporal asymmetry originating in the retinotectal visual pathway could propagate to and be modulated in higher areas in the visual cortex where cortical ERP components such as the N2pc and P_D are generated (but see Sylvester et al. 2007 for evidence that subcortically generated nasotemporal asymmetries do not necessarily propagate to higher visual cortical areas).

Finally, from an evolutionary perspective, an advantage for temporal visual events could be adaptively significant (Sylvester et al. 2007). Because temporal visual fields cover the far periphery of external visual space, a temporal visual hemifield advantage implies a bias toward orienting attention rapidly to stimuli in the far visual periphery. Organisms exhibiting such an advantage should be able to react faster to new and potentially relevant information in the far periphery, which is the area of the visual field where stimuli such as approaching predators will be registered first. Our results suggest that in specific situations where relevant information of a target object is to be attended in the face of distraction, this attentional advantage can be counteracted by appropriate inhibitory mechanisms.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: C.H.-H., A.G., U.A., and M.E. conception and design of research; C.H.-H. and A.G. performed experiments; C.H.-H. and A.G. analyzed data; C.H.-H., A.G., U.A., and M.E. interpreted results of experiments; C.H.-H. and A.G. prepared figures; C.H.-H. drafted manuscript; C.H.-H., A.G., U.A., and M.E. edited and revised manuscript; C.H.-H., A.G., U.A., and M.E. approved final version of manuscript.

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