Naso-Temporal ERP Differences:

Evidence for Increased Inhibition of Temporal Distractors

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Abstract

Previous research has demonstrated behavioral advantages for stimuli in the temporal visual hemifield relative to stimuli presented in the nasal hemifield. To investigate whether this naso-temporal asymmetry reflects a genuinely attentional bias towards the temporal visual field, we recorded event-related potentials (ERPs) in a task where participants had to identify a color-defined target digit in one visual hemifield that was accompanied by an irrelevant distractor in the opposite hemifield. To dissociate the processing of stimuli in the nasal and temporal visual hemifields, an eye patching procedure was employed. Target stimuli triggered N2pc components that mark the attentional selection of targets among distractors. Unexpectedly, these N2pc components were larger and emerged earlier for nasal relative to temporal targets. Experiment 2 provided evidence that this naso-temporal 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 (P_D component), resulting in more pronounced differences between contralateral and ipsilataral ERPs on trials with temporal distractors and nasal targets. These results provide novel evidence for a genuinely attentional naso-temporal asymmetry in the cortical processing of visual stimuli, and suggest that such asymmetries may be primarily associated with top-down controlled distractor inhibition.

Keywords: attention, visual hemifield, naso-temporal asymmetry, ERP, N2pc, inhibition

Introduction

The retino-geniculate and the retino-tectal pathways of the human visual system both contain crossed and uncrossed projections. Uncrossed projections remain on the same side as the visual field of stimulation, so that, for example, a stimulus in the left visual field is processed in the left geniculate body, cortical hemisphere, and superior colliculus (SC). In crossed pathways, visual information is projected to the contralateral side, so that a stimulus in the left visual field is processed in the right geniculate body, cortex, and SC. In humans, differences between crossed and uncrossed neural pathways have been investigated behaviorally with eye-patching procedures (e.g., Posner & Cohen, 1980). If one eye is patched, crossed and uncrossed pathways process visual information of the left and the right visual hemifield separately. For instance, if the left eye is patched, a stimulus on the left appears in the nasal visual field, is represented on the temporal hemiretina of the unpatched right eye, and is then projected via the uncrossed pathway. In contrast, a stimulus on the right 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 (see Figure 1).

Studies employing such an eye-patching procedure suggested that there are differences in the processing of input from the nasal compared to the temporal visual field (naso-temporal asymmetries). Using a choice saccade task, Posner and Cohen (1980) showed that humans preferentially orient towards signals in the temporal compared to the nasal visual hemifield. Subsequently, a similar temporal hemifield advantage has been replicated for manual response times (RTs) and saccade latencies, suggesting that the allocation of attention is faster or stronger for a stimulus in the temporal than in the nasal visual hemifield (Rafal et al., 1991). Other studies, however, failed to replicate such naso-temporal asymmetries for saccade latency (Bompas et al., 2008; Jóhannesson et al., 2012), and only replicated Posner and Cohen's initial observation that a higher proportion of saccades is directed to stimuli in the temporal compared to the nasal visual hemifield (Bompas et al., 2008).

Naso-temporal asymmetries have also been demonstrated for interference effects by irrelevant distractors. In a study on blindsight, Rafal et al. (1990) investigated distractor interference effects for a group of three hemianopic participants and a control group. They found that an irrelevant distractor in the blind temporal hemifield increased saccade latencies towards a target in the opposite hemifield more than did a distractor in the nasal visual hemifield. However, this effect was only present for the hemianopic participants, not for the control group, suggesting that naso-temporal asymmetries in distractor processing only emerge when hemianopic participants have to rely on their intact retino-collicular pathway. In a similar study, Walker, Mannan, Maurer, Pambakian, and Kennard (2000) found the opposite pattern of effects. In line with Rafal et al. (1990), a distractor in the temporal visual hemifield did interfere more than a nasal distractor. However, this asymmetry was only present in the control group, but not for a group of six hemianopic participants, suggesting an origin of the asymmetry in the retino-geniculate pathway (Walker et al., 2000). Although it is yet unclear why Rafal et al. (1990) and Walker et al. observed a qualitatively different dissociation pattern for naso-temporal asymmetries between hemianopic and fully-sighted participants, their observations converge in demonstrating that the location of task-irrelevant distractors in the temporal versus nasal visual hemifield can modulate the amount of interference produced by these distractors.

In sum, the existing literature suggests the existence of a naso-temporal asymmetry in visual attention, which may be due to a general attentional bias towards visual stimuli that appear in the temporal visual hemifield. From an evolutionary perspective, such an attentional 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 towards 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, the area of the visual field where stimuli such as approaching predators will be registered first.

The neural basis of such temporal hemifield advantages remains controversial. Whereas some authors argue that behavioral naso-temporal asymmetries reflect anatomical asymmetries in the phylogenetically older retinotectal pathway (Rafal et al., 1990, 1991), specifically in the superior colliculus (Sylvester et al., 2007), others have provided evidence against this view, and advocate geniculostriate or other cortical pathways (Bompas et al., 2008; Walker et al., 2000) as the source of these asymmetries. Rafal et al. (1990) have argued that temporal hemifield advantages found for a group of hemianopic participants was mediated by the retinotectal pathway, because of the lesions in the geniculostriate pathway for this group. In line with this hypothesis, anatomical studies on cats suggest that the retinotectal pathway exhibits a greater naso-temporal asymmetry than the geniculostriate pathway (Sterling, 1973). In macaques, the asymmetry in the retinotectal pathway is anatomically less well-defined but still existent (Hubel et al., 1975; Perry & Cowey, 1984). Newborns, in whom the geniculostriate pathway is not yet fully developed, exhibit a bias to saccade to stimuli in the temporal visual hemifield (Lewis & Maurer, 1992; Sireteanu et al., 1994). According to Rafal et al. (1991), these observations suggest that temporal hemifield advantages are mediated by more pronounced naso-temporal asymmetries within the retinotectal as compared to the geniculostriate pathway. The existence of functional naso-temporal asymmetries in the human midbrain was confirmed in an fMRI study by Sylvester et al. (2007), which demonstrated larger BOLD responses in the superior colliculus for stimuli in temporal compared to nasal hemifields following monocular visual stimulation, while cortical visual areas V1, V2, V3, and the lateral geniculate nucleus (LGN) did not show this asymmetry.

The hypothesis that temporal hemifield advantages are mediated primarily by the retinotectal geniculostriate visual pathway remains controversial. Williams, Azzopardi, and Cowey (1995) report that anatomically, reinotectal projections from the retina to the midbrain do not differ from retinogeniculate projections to the LGN in terms of their naso-temporal asymmetry. Similarly, Perry et al. (1984) found a naso-temporal asymmetry in the number of ganglion cells projecting to the LGN, with slightly more ganglion cells receiving input from the temporal compared to the nasal visual hemifield. Consistent with this anatomical finding, a

distractor in the temporal visual hemifield increased saccade latencies towards a target in the opposite hemifield more than a nasal distractor, but only for a group of eight control participants, not for a group of six hemianopic participants (Walker et al., 2000). Additional support for a cortical mediation of behavioral naso-temporal asymmetries is provided by Bompas et al., (2008), who used S-cone stimuli that are almost invisible to the retinotectal pathway and to the magnocellular layers of the LGN, and replicated Posner and Cohen's (1980) finding of preferential orienting towards the temporal compared to the nasal visual hemifield. This result suggests that naso-temporal asymmetries may also be generated within the geniculostriate pathway (Bompas et al., 2008).

In summary, existing evidence points towards attentional biases in favour of visual stimuli in the temporal hemifield. These biases can be uncovered in visual selection tasks when one eye is patched, where they are reflected by systematic differences in the impact of temporal versus nasal stimuli on manual and saccadic responses. The aim of the current study was to investigate whether such naso-temporal asymmetries are indeed linked to attentional biases, and whether such biases emerge early during the perceptual processing of visual stimuli by employing on-line electrophysiological markers of attentional target selection. Previous behavioral evidence for temporal-to-nasal hemifield differences comes mainly from choice saccade tasks (Bompas et al., 2008; Posner & Cohen, 1980), saccadic cueing tasks (Rafal et al., 1991), and distractor interference effects during saccade execution (Rafal et al., 1990; Walker et al., 2000). While these effects are consistent with differential attentional processing of nasal and temporal stimuli, they might also reflect biases that are generated at a later sensorimotor stage. Because stimulus position can automatically activate a motor response to the spatially compatible side (De Jong, Liang, & Hauber, 1996; Simon, 1969), naso-temporal asymmetries observed in saccade tasks may primarily reflect motor rather than an attentional effects (see, e.g., Ansorge, 2003). Although saccade preparation is linked to visuo-spatial attention (Deubel and Schneider, 1996; Hoffman and Subramaniam, 1995; Kowler et al., 1995; Kristjánsson et al., 2001; Kustov and Robinson, 1996), this link is less than perfect, as feature-based attentional search templates (e.g., for a specific color) are covertly deployed across the whole visual field

(Andersen, Fuchs, & Müller, 2010) even during saccade preparation (Born, Ansorge, & Kerzel, 2012). Therefore, markers of visuo-spatial attention in electroencephalography (EEG) data, such as the N2pc component (Eimer, 1996; Luck & Hillyard, 1994) would provide more direct and unequivocal evidence for a genuinely *attentional* naso-temporal hemifield asymmetry, and would also shed light on the neural time course of such effects.

To test whether a temporal hemifield advantage is due to an *attentional* benefit for the temporal compared to the nasal visual hemifield, we measured the N2pc component as an indicator of spatially selective attention for targets in the temporal and the nasal visual field. The N2pc reflects an enhanced negativity difference of the event-related potential (ERP) at posterior electrodes contralateral to the visual field of a target stimulus relative to ipsilateral electrodes. It has its maximum at about 180 to 230 ms after target onset over the posterior scalp and is supposed to indicate the attentional selection of a target stimulus among distractors (Luck and Hillyard, 1994; Eimer, 1996). To assess the naso-temporal asymmetry of the N2pc, we used a task where participants reported the identity of a color-defined target digit that was presented to the left or to the right of fixation together with a task-irrelevant distractor stimulus in the opposite visual field (see Figure 1). In this task, target stimuli have previously been shown to elicit robust N2pc components (Grubert and Eimer, 2013). To dissociate N2pc components to target stimuli presented in the temporal or nasal visual field, a block-wise eye-patching procedure was employed. In different blocks, participants performed the task with their left eye or their 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 on separate hemiretinae (see Figure 1). When the right eye was open (and the left eye was patched), stimuli on the left side appeared in the nasal visual hemifield and projected to the temporal hemiretina, while a stimulus 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.

This combination of eye-patching and the lateral presentation of target and distractor objects on opposite sides can isolate the contributions of temporal and nasal projections to the target-elicited N2pc components, due to the mirror-reversed representation of the visual field on the retinae (such that an object on the left is presented on the right retinae of both eyes) and the partial crossing of each eye's retinal projections (such that the nasal hemiretinae project to the contralateral brain side, whereas the temporal hemiretinae project to the ipsilateral brain side). The temporal N2pc can be computed by combining trials from blocks where the left eye is patched and targets appear on the right side, and from blocks where the right eye is patched and targets appear on the left side. Analogously, the nasal N2pc can be obtained by combining left target/left eye patch and right target/right eye patch trials. As the N2pc is an established ERP marker of spatially selective attentional target processing (Eimer, 1996; Luck and Hillyard, 1994), an attentional advantage for target stimuli in the temporal visual hemifield should be reflected by larger and/or earlier N2pc components for temporal as compared to nasal targets.

Experiment 1

Methods

Participants

Thirteen paid volunteers participated in Experiment 1. One was excluded because of excessive blinks and eye movements. The mean age of the 12 remaining participants was 32.8 years, ranging from 24 to 46 years. Six participants were female and one was left-handed. Written informed consent was obtained from the participants prior to the experiment. All participants had normal or corrected to normal vision and color vision.

Stimuli and Procedure

Stimuli were presented on a 22-inch Samsung wide SyncMaster 2233 LCD monitor with 5 ms response time at a resolution of 1,280 × 1,024 pixel and a 100 Hz refresh rate. Stimulus

presentation and response collection were controlled by a PC running under Windows XP using Matlab (Mathworks, Inc.) and the Cogent 2000 and Cogent Graphics toolboxes (Cogent 2000 team and John Romaya, UCL, London, UK). Participants viewed the screen from a distance of 80 cm.

Stimuli were presented for 150 ms against a black background. A central grey 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 Figure 1A). 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 non-target colors. In each trial, one of the digits had the target color, and the other digit had one of the non-target colors. Non-target 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 *left eye patched* and the *right eye patched* condition. On the basis of these viewing conditions, three types of visual field conditions were computed (see Figure 1B). 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 leftt targets in right eye patched blocks. Participants performed three successive blocks of 66 trials in each viewing condition (no patch, left eye patched, right eye patched), resulting in an equal number of trials in

each visual field condition (full visual field, temporal target, nasal target). The sequence of viewing conditions was counterbalanced across participants.

Trials were separated by an interval of 1,650 ms. 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 prior to the first experimental block.

---------- Insert Figure 1 about here ----------

EEG Data Recording and Analysis

The continuous EEG was DC-recorded from 64 electrodes placed in an elastic cap according to the standard 10/10-electrode system. 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 re-referenced to the average of both earlobes. Trials were segmented from 100 ms before to 600 ms after stimulus onset, and ERPs were computed relative to a 100 ms pre-stimulus baseline. Trials including eye movements (±30 μV at HEOG channels) or blinks (±60 μV at Fp1/2) were removed from further analysis. For trials including muscular artefacts (±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. EEG was averaged for each combination of viewing condition (no patch, left eye patched, right eye patched) and side of target digit (left, right). In a second step, 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 target digits were quantified on the basis of mean amplitudes in a 190 – 280 ms post stimulus time window at lateral posterior electrode sites PO7 and PO8. N2pc onset latencies were determined on the basis of difference waveforms (subtracting ERPs ipsilateral to the target from contralateral ERPs). Twelve subsamples of grand-averaged difference waves were computed in which always one participant in turn was excluded from the subsample scores to obtain jackknifed difference waves (Miller, Patterson, & Ulrich, 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 a repeated measures analysis of variance (ANOVA) and follow-up *t*-tests, for which *F*- and *t*-values were corrected according to the formula 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.

Results

Behavioral Results

Trials faster than 200 ms or slower than 1,500 ms were excluded from the analysis (0.1% of all trials). Response times (RTs) were subjected to a repeated measures ANOVA with the variable visual field of target (full visual field, target in temporal hemifield, target in nasal hemifield), which revealed a main effect [$F(2,22) = 11.62$, $p < .001$]. Follow-up *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 in the nasal visual hemifield [565 ms, $t(11) = 4.08$, $p < 0.01$]. RTs between the two hemifield conditions (nasal vs. temporal) did not differ [$t(11) < 1.00$]. Analogous results were obtained in an additional ANOVA with the factor viewing condition (no eye patch, left eye patched, right eye patched), which obtained a main effect [$F(2,22) = 10.14$, $p < 0.001$]. Responses in the no eye patched condition (546 ms) were faster compared to the right

eye patched [566 ms, $t(11) = 3.71$, $p = 0.01$] or left eye patched condition [564 ms, $t(11) = 3.44$, $p = 0.02$]. The latter two conditions 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%, temporal target: 2.9%), and there was no effect of visual field on error rates [$F(2,22) < 1$].

ERP Results

Figure 2A shows grand average ERPs measured at electrode sites PO7/8 contralateral and ipsilateral to the side of a target stimulus, separately for the three visual field conditions (full visual field, target in temporal hemifield, target in nasal hemifield). A solid N2pc was triggered in all three conditions. However, and unexpectedly, the N2pc to targets in the temporal visual hemifield was smaller relative to the N2pc in response to 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 Figure 2B, which 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, but the N2pc to targets in the nasal hemifield tended to be larger.

This pattern of N2pc results was statistically confirmed by a repeated measures ANOVA with the factors visual field of target (full visual field, temporal target, nasal target) and laterality (electrode contralateral versus ipsilateral to the side of the target digit), carried out on mean amplitudes measured in the 190-280 ms post-stimulus 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 the 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 [$t(11) = 3.6$, $p = .012$]. 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 [$t(11) = 2.2$, $p = 0.16$], or to targets in the nasal hemifield [$t(11) = 2.1$, $p = 0.17$].

To assess N2pc onset latency differences between full-field, nasal, and temporal targets, jackknife-based N2pc onset latency estimates were subjected to a repeated measures ANOVA, which revealed a main effect of visual field of target [$F_c(2,22) = 8.9$, $p = .004$]. Follow-up *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, $t_c(11) = 3.2$, $p = .025$], and relative to the target N2pc in the full visual field condition [181 ms, $t_c(11) = 3.6$, $p = .013$]. There was no N2pc onset latency difference between nasal-hemifield targets and targets in full visual field blocks [$t_c(11) < 1.00$].

To illustrate the effects of monocular versus binocular viewing conditions on non-lateralized visual ERP components, Figure 3 shows ERPs at lateral posterior electrodes (averaged across PO7 and PO8) in full visual field blocks (solid line) and in 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 viewing conditions. This was confirmed by two independent t-tests on P1 and N1 peak latencies (obtained within an 80-160 ms and a 150-250 ms post-stimulus time window, respectively). Compared to blocks in which one eye was patched, both the P1 (138 ms versus 117 ms) as well as the N1 component (190 ms versus 180 ms) peaked earlier in full-view blocks, both $t(11) > 4.1$, $p < .003$.

---------- Insert Figure 2 and 3 about here ----------

Discussion

To investigate whether the naso-temporal asymmetry observed in previous behavioral experiments is generated at the stage of attentional target selection, we employed an eye patching procedure and measured N2pc components to targets in the temporal or nasal visual hemifield, as well as target N2pc components in full-view blocks without eye patching. Our N2pc

results did indeed reveal the existence of an attentional naso-temporal asymmetry, with systematic differences of N2pc components in response to temporal versus nasal target stimuli. However, the direction of this asymmetry was opposite to our predictions. We assumed that a temporal hemifield advantage would lead to a larger and earlier N2pc for targets in the temporal compared to targets in the nasal visual hemifield. Results revealed the reverse pattern, namely a reduced and delayed N2pc for targets in the temporal compared to targets in the nasal visual hemifield.

To account for this unexpected finding, it is useful to consider possible links between naso-temporal asymmetries and distractor inhibition processes. Naso-temporal asymmetries are usually not found for responses to targets presented in isolation (Jóhannesson et al., 2012), but instead in contexts where targets are accompanied by distractors at the opposite side, and there are systematic differences in the interference produced by temporal as compared to nasal distractor objects (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, attentional target selection may require a greater degree of inhibition of temporal as compared to nasal distractors. This possibility is important for the interpretation of the surprising pattern of N2pc results observed in Experiment 1, because the N2pc component reflects both target facilitation *and* distractor inhibition (Hickey et al., 2009). Under conditions where a target and a distractor are simultaneously presented on opposite sides, the N2pc component does not only represent an enhanced negativity contralateral to the target that is associated with target selection, but it also includes an additional positive deflection (P_D component) contralateral to the distractor that has been associated with distractor inhibition processes (Hickey et al., 2009). If the N2pc reflects the additive contribution of both target selection and distractor inhibition, N2pc results of Experiment 1 could be primarily driven by a naso-temporal 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 was designed to test the hypothesis that temporal distractors trigger a larger inhibition-related P_D component than nasal distractors.

Another notable finding of Experiment 1 was the delay of early visual P1 and N1 components under monocular relative to binocular viewing conditions (Figure 3), 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, response times 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 approximately 10-20 ms longer until this activation level is reached. The observed response time 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 as compared to binocular viewing conditions.

Experiment 2

The aim of Experiment 2 was two-fold. First, we wanted to replicate the unexpected finding of a larger N2pc to targets in the nasal compared to the temporal visual hemifield. Second, we tested the hypothesis that this difference can be accounted for by differences in the P_D towards temporal versus nasal distractors. Such a P_D difference would indicate increased inhibition of a distractor in the temporal compared to the nasal visual hemifield, and would be in line with research on naso-temporal asymmetries that highlights stronger interference effects for temporal versus nasal distractors (Rafal et al., 1989; Berger and Henik, 2000; Walker et al., 2000). If temporal distractors elicit stronger P_D components than nasal distractors, this P_D

should result in an overall increase of the N2pc observed in trials with nasal targets and temporal distractors relative to trials with temporal targets and basal distractors (see Hickey et al., 2009, for a demonstration of the additive effects of target selection and distractor inhibition on N2pc components).

To test this hypothesis, we modified the task of Experiment 1 and introduced distractor-only trials. Distractor-only displays 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. The presence of two distractors allowed us to directly compare the EEG signal to temporal and nasal distractors and, therefore, it allowed us to determine the presence of larger P_D components for temporal relative to nasal distractors. 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. Note that for this kind of trials, 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 contra 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 that were identical to Experiment 1. In line with the observations from this experiment, we expected that the N2pc to a temporal target (accompanied by a nasal distractor) would be reduced compared to the N2pc elicited by a nasal target (accompanied by a temporal distractor). 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 the nasal N2pc in target-distractor trials, this would provide an explanation for the more pronounced N2pc to nasal compared to temporal targets.

Methods

Participants

Eight paid participants (5 female, 2 left-handed) performed Experiment 2 after giving written informed consent. Their mean age was 32 years, ranging from 26 to 40 years. All of them had normal or corrected to normal vision and color vision.

Stimuli and Procedure

Stimuli, apparatus and procedure were the same as 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. 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 5 left-eye-patched and the 5 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, and the computation of N2pc waveforms for temporal and nasal targets on target-distractor trials was 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 ipsilateral electrode on distractor-only trials. In blocks where the left eye was patched, these labels were reversed. In the combined ERP waveforms for distractor-only trials, maintaining electrode laterality (contralateral versus ipsilateral) was therefore always defined relative to the temporal distractor item. As in Experiment 1, N2pc

onset latencies estimate were determined with the jack-knife procedure by Miller et al. (1998; see also Ulrich & Miller, 2001), employing the same fixed threshold of 0.5μV.

Results

Behavioral Results

Trials with incorrect responses and trials with responses faster than 200 ms or slower than 1500 ms were excluded from the analysis (< 0.02 % of all trials). A paired *t*-test indicated no significant difference between responses to temporal (620 ms) vs. 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

As can be seen from Figure 4A, targets in the temporal and in the nasal visual hemifield both elicited N2pc components. As in Experiment 1, the N2pc was larger for targets in the nasal compared to the temporal visual field. A repeated measures ANOVA with the variables visual field (target in temporal hemifield, target in nasal hemifield) and laterality (electrode contralateral versus ipsilateral to the targets) on ERP mean amplitudes measured at PO7/8 in the 190-280 ms post-stimulus 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 to temporal targets [Visual Field × Laterality interaction, $F(1,7) = 9.97$, $p = 0.02$]. As can be seen in the contralateral-ipsilateral N2pc difference waves in Figure 4B, the N2pc to temporal targets was not only attenuated, but also numerically delayed relative to the N2pc to nasal targets (204 ms versus 184 ms), similar to the N2pc latency shift observed in Experiment 1. However, this difference was not statistically significant [$t_c(7) < 1.00$].

Critically, as predicted by the naso-temporal asymmetry accounting for distractor inhibition, an enhanced positivity (P_D component) was elicited on distractor-only trials contralateral to temporal distractors (Figure 4A, rightmost panel). 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 (Figure 4B, dashed line). Although small in size, this P_D component was 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 (190-280 ms post-stimulus) confirmed that the P_D component was statistically reliable [$t(7) = 2.51$, $p = 0.04$].

---------- Insert Figure 4 and 5 about here ----------

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. Importantly, the analysis of distractor-only trials provided support for our hypothesis that this naso-temporal 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 distractors 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 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 naso-temporal 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 naso-temporal N2pc asymmetry observed on

target-distractor trials was considerably larger than the naso-temporal P_D asymmetry measured on distractor-only trials (see Figure 4B).

The topographical maps in Figure 5 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 (190-280 ms post-stimulus) 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 component overlap in terms of their scalp distributions (Hickey et al., 2009).

General Discussion

The results of this study provide novel ERP evidence for the existence of a genuinely attentional naso-temporal asymmetry. However, the direction of this asymmetry was unexpected. Based on the temporal hemifield advantage observed in earlier behavioral studies (e.g., Rafal et al., 1991), we expected to find a more pronounced N2pc to targets in the temporal as compared to the nasal visual field. However, Experiment 1 showed that the N2pc to temporal targets was in fact reduced in size compared to nasal targets. This finding was replicated in Experiment 2. In addition, 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., 2009), this results suggests that temporal distractors are inhibited more strongly than nasal distractors. This naso-temporal 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 a greater amount of attentional inhibition, resulting in larger P_D components , because they are generally more likely to capture attention than nasal distractors. Overall, our results suggest that instead of being an attentional advantage for *targets* in the temporal hemifield, naso-temporal asymmetries may be better conceived of as a reduced ability of nasal *distractors* to capture attention, resulting in faster and/or easier inhibition of nasal as compared to temporal distractors. This inhibition account of temporal hemifield advantages is in line with previous observations of naso-temporal asymmetries in distractor interference effects. Walker et al. (2000) found increased distractor interference for temporal compared to nasal distractors, reflected by slower saccade latencies, but only for a control group and not for hemianopic participants. This difference between patients and controls led Walker et al. to conclude that cortical visual areas mediate naso-temporal asymmetries. The experimental design of Walker et al. (2000) 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 towards temporal and nasal targets did not differ, suggesting an important role of distractors for naso-temporal asymmetries. Our result of a greater P_D for temporal compared to nasal distractors is in line with these observations, as it suggests increased inhibition for temporal compared to nasal distractors. 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 as compared to nasal distractors, but only for hemianopic participants and not for healthy controls, indicative of an involvement of subcortical pathways in naso-temporal 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 to the nasal visual field, and this may be directly linked to our finding that temporal distractors trigger larger inhibition-related P_D components.

Although our data provide ERP evidence for an attentional naso-temporal asymmetry in distractor processing, there were no systematic behavioral differences between trials with temporal targets and nasal distractors and trials with nasal targets and temporal distractors in either Experiment 1 or Experiment 2. If temporal distractors are more likely to attract attention and therefore require stronger inhibition, this might have been reflected by delayed responses to nasal targets relative to trials with nasal distractors and temporal targets. Such a pattern of results was observed by Rafal et al. (1991) in an exogenous cueing task, where temporal hemifield advantages were found for response times and saccade latencies. Because Rafal et al. analyzed the data of their cueing task in terms of a hemifield advantage for cues, and did not analyze responses to temporal and nasal targets per se within each cue condition (valid, neutral, invalid), their findings indicate a temporal hemifield advantage for distracting cues rather than for targets. Our result of an increased need for inhibiting temporal distractors is in line with larger spatial cueing effect for distracting cues in the temporal hemifield (Rafal et al., 1991), which may reflect incomplete inhibition of these cues. The question remains why similar behavioral differences between trials with temporal and nasal distractors were not observed in the present study. One possibility is that the strong attentional inhibition of temporal distractors, as reflected by the P_D component, was successful in preventing any interference of these distractors on the attentional selection and identification of target items in the opposite nasal hemifield. Certain procedural differences between our task and the exogenous cueing task of Rafal et al. (1991) support this interpretation. While target and distractor had different colors in our study, cue and targets were both grey-scale stimuli in Rafal et al. (1991), and were

therefore more similar to each other. Because distractor inhibition works better when target and distractor objects are dissimilar (Ansorge, Priess, & Kerzel, 2013), it is likely that the cue/distractor could be inhibited more successfully in our study task than in the task of Rafal et al (1991). In addition, distractor inhibition may generally be more successful when targets and distractors are presented simultaneously (as in the current study) than when they are separated in time (as in Rafal et al., 1991).

Apart from suggesting that temporal hemifield advantages are linked to an increased suppression of temporal compared to nasal distractors, and may therefore not be directly linked to benefits on the attentional processing of temporal target stimuli, our finding that naso-temporal asymmetries can be observed for cortical ERP components such as the N2pc and the P_D strongly suggests that these asymmetries are at least in part generated at cortical levels of visual processing (cf. Walker et al., 2000; Bompas et al., 2008). 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 towards stimuli in the temporal hemifield (Posner & Cohen, 1980). This demonstrates that naso-temporal 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). Similarly, Walker et al. (2000) found a naso-temporal asymmetry in distractor interference effects for normal subjects, but not for hemianopic patients in which parts of the geniculostriate pathway were severed, suggesting a role of cortical areas for naso-temporal asymmetries (Walker et al., 2000). However, it remains possible that this asymmetry is present at cortical stages of visual processing, but still arises from subcortical structures. Neuroanatomical studies provide 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 naso-temporal asymmetry has been reported for the retinotectal (Perry and Cowey, 1984) pathway, *and* for projections to the LGN (Perry et al., 1984). A naso-temporal asymmetry originating in the retinotectal visual pathway might propagate to higher areas in visual cortex where it gives rise to systematic modulations of cortical ERP components such as the N2pc and the P_D. However, the fact that Sylvester et al. (2007) found higher fMRI

signal changes in the superior colliculus (tectum) for stimulation from the temporal compared to the nasal visual hemifield, but no such asymmetry in LGN, V1, V2, and V3, suggests that naso-temporal asymmetries at subcortical processing stages do not neccesarily propagate to higher visual cortical areas.

An important difference between the study of Sylvester et al. (2007) and our experiments is the mode of stimulation. While Sylvester et al. stimulated each hemifield (nasal and temporal) separately, our stimulus displays were perceptually balanced and always contained two stimuli in opposite hemifields. Sylvester et al. (2007) may have revealed genuinely low-level differences in the subcortical sensory processing of stimuli in the temporal versus nasal visual field, while our study investigated a situation where there is attentional competition between simultaneously present target and distractor objects. In such contexts, there are indeed attentional advantages for target objects in the temporal versus nasal visual field. The findings of the present study suggest that these advantages may not primarily be due to a preferential processing of target stimuli in the temporal field, but are related to a stronger need to inhibit temporal as compared to nasal distractors. The observations of Sylvester et al. (2007) suggest that there may be a generic bottom-up bias in the sensory processing of visual events towards the temporal hemifield, and this may be directly linked to the stronger top-down attentional inhibition of a temporal distractor observed in the present study. If visual stimuli in the temporal hemifield generally elicit stronger neural responses than nasal stimuli, attentional control processes that facilitate target selection through distractor suppression need to be activated more strongly under conditions where a temporal distractor is accompanied by a task-relevant target object in the nasal visual field.

Author Contributions

Conceived and designed the experiments: CHH, AG, UA, ME. Performed the experiments: CHH, AG. Analyzed the data: CHH, AG. Wrote the paper: CHH, AG, UA, ME.

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References

Ansorge U. Asymmetric influences of temporally versus nasally presented masked visual information: Evidence for collicular contributions to nonconscious priming effects. *Brain Cogn.* 51: 317-325, 2003.

Ansorge U, Priess, HW, Kerzel, D. Effects of relevant and irrelevant color singleton on inhibition of return and attentional capture. *Attent. Percept. Psychoph.* 75: 1687-1702, 2013.

Andersen SK, Fuchs S, Muller MM. Effects of feature-selective and spatial attention at different stages of visual processing. *J. Cogn. Neurosci.* 23: 238–246, 2010.

Berger A, Henik A. The endogenous modulation of IOR is nasal-temporal asymmetric. *J. Cogn. Neurosci.* 12: 421–8, 2000.

Bompas A, Sterling T, Rafal RD, Sumner P. Naso-temporal asymmetry for signals invisible to the retinotectal pathway. *J. Neurophysiol.* 100: 412–421, 2008.

Born S, Ansorge U, Kerzel D. Feature-based effects in the coupling between attention and saccades. *J. Vision* 12(11): 27, 2012.

De Jong R, Liang CC, Lauber E. Conditional and unconditional automaticity: A dual-process model of effects of spatial stimulus–response correspondence. *J. Exp. Psychol. Hum. Percept. Perform.* 20: 731–750, 1996.

Deubel H, Schneider WX. Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res.* 36: 1827–37, 1996.

Eimer M. The N2pc component as an indicator of attentional selectivity. *Electroencephalogr. Clin. Neurophysiol.* 99: 225–34, 1996.

Grubert A, Eimer M. Qualitative differences in the guidance of attention during single-color and multiple-color visual search: Behavioral and electrophysiological evidence. *J. Exp. Psychol. Hum. Percept. Perform.* 39: 1433–1442, 2013.

Hickey C, Di Lollo V, McDonald JJ. Electrophysiological indices of target and distractor processing in visual search. *J. Cogn. Neurosci.* 21: 760–775, 2009.

Hoffman JE, Subramaniam B. The role of visual attention in saccadic eye movements. *Percept. Psychophys.* 57: 787–795, 1995.

Hubel DH, LeVay S, Wiesel TN. Mode of termination of retinotectal fibers in macaque monkey: An autoradiographic study. *Brain Res.* 96: 25–40, 1975.

Jóhannesson OI, Asgeirsson AG, Kristjánsson A. Saccade performance in the nasal and temporal hemifields. *Exp. Brain Res.* 219: 107–20, 2012.

Kowler E, Anderson E, Dosher B, Blaser E. The role of attention in the programming of saccades. *Vision Res.* 35: 1897–916, 1995.

Kristjánsson Á, Chen Y, Nakayama K. Less attention is more in the preparation of antisaccades, but not prosaccades. *Nat. Neurosci.* 4: 1037–1042, 2001.

Kustov AA, Robinson DL. Shared neural control of attentional shifts and eye movements. *Nature* 384: 74–77, 1996.

Lewis TL, Maurer D. The development of the temporal and nasal visual fields during infancy. *Vision Res.* 32: 903–911, 1992.

Luck SJ, Hillyard SA. Spatial Filtering During Visual Search: Evidence From Human Electrophysiology. *J. Exp. Psychol. Hum. Percept. Perform.* 20: 1000–1014, 1994.

Miller J, Patterson T, Ulrich R. Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology* 35: 99–115, 1998.

Perry VH, Cowey A. Retinal ganglion cells that project to the superior colliculus and pretectum in the macaque monkey. *Neuroscience* 12: 1125–37, 1984.

Perry VH, Oehler R, Cowey A. Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. *Neuroscience* 12: 1101–23, 1984.

Posner MI, Cohen Y. Attention and the Control of Movements. In: *Tutorials in Motor Behavior*, edited by Stelmach GE, Jean Requin. Amsterdam: North-Holland Publishing Company, 1980, p. 243–258.

Rafal R, Henik A, Smith J. Extrageniculate Contributions to Reflex Visual Orienting in Normal Humans : A Temporal Hemifield Advantage. *J. Cogn. Neurosci.* 3: 322–328, 1991.

Rafal R, Smith J, Krantz L, Cohen A, Brennan C. Extrageniculate vision in hemianopic humans: saccade inhibition by signals in the blind field. *Science (80-.).* 250: 118–121, 1990.

Rafal RD, Calabresi PA, Brennan CW, Sciolto TK. Saccade preparation inhibits reorienting to recently attended locations. *J. Exp. Psychol. Hum. Percept. Perform.* 15: 673–685, 1989.

Simon JR. Reactions towards the source of stimulation. *J. Exp. Psychol.* 81: 174–176, 1969.

Sireteanu R, Fronius M, Constantinescu DH. The development of visual acuity in the peripheral visual field of human infants: binocular and monocular measurements. *Vision Res.* 34: 1659–1671, 1994.

Sterling P. Quantitative mapping with the electron microscope: retinal terminals in the superior colliculus. *Brain Res.* 54: 347–354, 1973.

Sylvester R, Josephs O, Driver J, Rees G. Visual fMRI Responses in Human Superior Colliculus Show a Temporal – Nasal Asymmetry That Is Absent in Lateral Geniculate and Visual Cortex. *J. Neurophysiol.* 97: 1495–1502, 2007.

Ulrich R, Miller J. Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology* 38: 816–27, 2001.

Walker R, Mannan S, Maurer D, Pambakian ALM, Kennard C. The oculomotor distractor effect in normal and hemianopic vision. *Proc. R. Soc. B. Biol. Sci.* 267: 431–8, 2000.

Williams C, Azzopardi P, Cowey A. Nasal and temporal retinal ganglion cells projecting to the midbrain: Implications for "Blindsight."*Neuroscience* 65: 577–586, 1995.