

Electroencephalographic evidence of vector inversion in antipointing

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Abstract Mirror-symmetrical reaching movements (i.e., antipointing) produce a visual-field-specific pattern of endpoint bias consistent with a perceptual representation of visual space (Heath et al. in *Exp Brain Res* 192:275–286, 2009a; *J Mot Behav* 41:383–392 2009b). The goal of the present investigation was to examine the concurrent behavioural and event-related brain potentials (ERP) of pro- and antipointing to determine whether endpoint bias in the latter task is related to a remapping of the environmental parameters of a target (i.e., *vector inversion hypothesis*) or a shift of visual attention from a veridical to a cognitively represented target location (i.e., *reallocation of attention hypothesis*). As expected, results for antipointing—but not propointing—yielded a visual-field-specific pattern of endpoint bias. In terms of the ERP findings, an early component (i.e., the N100) related to the orienting of visuospatial attention was comparable across pro- and antipointing. In contrast, a later occurring component (i.e., the P300) demonstrated a reliable between-task difference in amplitude. Notably, the P300 has been linked to the revision of a ‘mental model’ when a mismatch is noted between a stimulus and a required task goal (so-called context-updating). Thus, we propose that the between-task difference in the P300 indicates that antipointing is

associated with a remapping of a target’s veridical location in mirror-symmetrical space (i.e., vector inversion). Moreover, our combined behavioural and ERP findings provide evidence that vector inversion is mediated via perception-based visual networks.

Keywords Action · Antipointing · Event-related brain potential · Reaching · Perception · Propointing

Introduction

Reaching and grasping movements typically involve dimensional overlap between stimulus and response (i.e., propointing) and are associated with maximally efficient and effective motor output (Fitts and Seeger 1953; Kornblum et al. 1990). Convergent evidence suggests that propointing responses exhibit optimized motor performance due to their mediation via the stimulus-driven visuomotor networks of the dorsal visual pathway that operate independent of cognitively derived principles (for recent review see Goodale 2011). It is, however, important to recognize that individuals are able to decouple the spatial relations between stimulus and response and implement an action in a direction other than the cued stimulus (i.e., non-standard task). Indeed, non-standard tasks represent an intriguing area of inquiry because they provide a basis for understanding how cognitive principles influence visuomotor control. One non-standard task that our group has explored is the antipointing paradigm. In this paradigm, participants reach mirror-symmetrical (i.e., 180° spatial transformation) to an exogenously or endogenously presented target in the horizontal plane. Results from this paradigm have shown that antipointing produces longer reaction times than their propointing counterparts (Carey

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et al. 1996; Chua et al. 1992) and elicit a visual-field-specific pattern of endpoint bias. In particular, left and right space antipointing under- and overshoot veridical target location, respectively, and this pattern characterizes both left- and right-hand reaches (Heath et al. 2009a, b; Maraj and Heath 2010).

In terms of explaining the increased reaction times and endpoint bias of antipointing, our group has drawn upon the *vector inversion* and the *reallocation of attention hypotheses* developed from the extensive antisaccade literature. Both models contend that antisaccades entail a two-component process requiring the top-down inhibition of a stimulus-driven response (i.e., response suppression). Following response suppression, the vector inversion hypothesis contends that a *visual* remapping of target parameters to a mirror-symmetrical location in space is required to produce the response's appropriate 'anti' coordinates (for review see Munoz and Everling 2004). Evidence supporting the visual nature of vector inversion stems from work showing that a subset of visually responsive cells in the parietal cortex (i.e., area LIP) exhibit alternative receptive fields: one standard visual field establishing the veridical coordinates of a target and a non-standard field reflecting the target's mirror-symmetrical location (Zhang and Barash 2000; see also Zhang and Barash 2004).¹ Importantly, Zhang and Barash argue that some 'context-categorization process' (p. 974) is responsible for the switch between the standard and the non-standard receptive fields and that such a process occurs in advance of movement planning. In contrast, the reallocation of attention hypothesis holds that response suppression is followed by a process of orienting attention away from the target stimulus and towards the required 'anti' location (Olk and Kingstone 2003). More specifically, Olk and Kingstone argue that 'anti' tasks require the time-consuming process of moving covert attention to separate locations in visual space. Thus, the vector inversion hypothesis contends that a visual remapping between stimulus and response allows for an appropriate sensory-to-motor transformation, whereas the reallocation of attention hypothesis asserts a unitary shift of visual attention from a 'pro' to an 'anti' coordinate.

Of course, antipointing also requires the suppression of a stimulus-driven response as well as vector inversion and/or attention reallocation; thus, the aforementioned hypotheses provide viable frameworks for explaining the increased latencies of antipointing. Further, the fact that both vector inversion and attention reallocation are defined as obligatory

and top-down processes provide a parsimonious explanation for the visual-field-specific bias of antipointing. In particular, our group (Heath et al. 2009b; Maraj and Heath 2010) has proposed that the intentional process of vector inversion and/or attention reallocation disrupts the online control of visuo-motor networks and results in the processing of target features (i.e., extent) via the perceptual networks of the ventral visual pathway (Goodale 2011). This explanation is in line with well-documented evidence that obligatory judgments of stimulus properties (e.g., size, extent, numerosity and brightness) are over- and underestimated in left and right visual fields, respectively (Charles et al. 2007; Nicholls et al. 1999). Therefore, antipointing responses directed in the left visual field (i.e., a response cued by a target presented in the right visual field) elicit an undershooting bias because the target's veridical location is underestimated, whereas antipointing in the right visual field (i.e., a response cued by a target presented in the left visual field) produces an overshooting bias because the target's veridical location is overestimated.

To our knowledge, Connolly et al.'s (2000) fMRI study represents the only work to characterize the neural systems underlying antipointing. Their work showed that antipointing (performed without a concomitant antisaccade) engaged the same inferior parietal networks as antisaccades and was additionally related to the activation of a superior parietal region—a region that further research has identified as the parietal reach region (Connolly et al. 2003; see Buneo et al. 2002). Moreover, that antipointing engaged in additional parietal networks was interpreted to reflect the increased computation demands of transforming 'anti' coordinates into an appropriate hand-centred frame of reference. Notably, however, Connolly et al.'s study was not designed to examine the contemporaneous behavioural and electrophysiological properties of antipointing nor to evaluate the competing predictions of the vector inversion and reallocation of attention hypotheses. To that end, the present study contrasted the behavioural findings and event-related brain potentials (ERP) of pro- and antipointing in a cuing paradigm wherein information related to task type (i.e., propointing vs. antipointing) and target location was provided in advance (i.e., 1,000 ms) of response cuing. Because the aforementioned information was provided prior to response cuing, both pro- and antipointing required equivalent response suppression. As such, the present experiment provides a specific basis to address the role of vector inversion and/or attention reallocation in the control of antipointing (see also Heath et al. 2009b).

A priori, we identified the N100 and the P300 as candidate ERP components associated with the reallocation of attention and vector inversion, respectively. Specifically, the N100 component has a lateralized posterior scalp topography and is sensitive to the allocation of visuospatial attention (Handy et al. 2001). For example, the N100 has

¹ Zhang and Barash's (2000) non-human primate electrophysiology study observed 185 units in LIP that elicited a strong visual response to the onset of a stimulus. Of these neurons, 30 % demonstrated a shift in activity from the visual to the motor direction of an upcoming antisaccade.

been shown to be sensitive to target-related attentional changes in perceptual and motor processing when participants are asked to distinguish between target and non-target items (Couperus 2010; Handy et al. 2001; Krigolson et al. 2008; Ritter et al. 1982). Moreover, manipulating the perceptual load (i.e., attentional resources) that must be devoted to a cued target location reliably influences the N100 amplitude (Handy and Mangun 2000; Mangun and Hillyard 1991). In other words, the N100 has been linked to early spatial selection in visual processing. Thus, if anti-pointing is associated with a unitary shift of visual attention from ‘pro’ to ‘anti’ coordinates (i.e., the reallocation of attention hypothesis) than tasks should differ in terms of N100 amplitude or lateralization.

The P300 is a later occurring and parietally distributed ERP component that has been linked to the top-down updating of an internal environmental representation (so-called context-updating) (Donchin and Coles 1988). More specifically, the P300 has been shown to relate to the revision of a ‘mental model’ when a mismatch exists between a stimulus and a required response (see also Nieuwenhuis et al. 2005). For example, in the goal-directed reaching literature, a larger P300 waveform has been reported in response to an unexpected ‘jump’ in target location. In this context, the P300 is thought to reflect the required updating of an internal movement model necessary to achieve the spatial coordinates of the new target location (Krigolson et al. 2008; see also Krigolson et al. in press). Thus, a reliable difference in the P300 component across pro- and anti-pointing would support the assertion that a visual inversion of the spatial relations between target and response supports anti-pointing (i.e., the vector inversion hypothesis).

Methods

Participants

Twelve right-handed individuals (18–24 years of age; 6 male, 6 female) with normal or corrected-to-normal vision participated in the experiment. Participants provided informed consent approved by the Office of the Vice-President, Research, University of Victoria, and this study was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Apparatus and procedures

Participants were seated in front of an aiming apparatus that consisted of a two-sided box (740 mm high, 960 mm wide and 600 mm deep) divided in half by a fully silvered mirror inclined at 20°. A 17-inch computer monitor (LG 1750 SQ, 8-ms response rate) was placed upside down on

the superior surface of the apparatus and was used to project visual stimuli onto the surface of the mirror. The distance between the eyes and the mirror was approximately 450 mm. A graphics tablet (WACOM Intuos 2, 300 mm × 450 mm; sampling rate, 125 Hz) was placed directly below the mirror such that movements made on the surface of the graphics tablet via a stylus corresponded to unitary movement of a cursor (5-mm-radius circle) appearing on the surface of the mirror. All computer events and experimental stimuli were controlled via MATLAB (7.6: The MathWorks, Natick, MA, USA) and the Psychophysics Toolbox extensions (Brainard 1997).

Participants held the stylus in their right hand and reached to visually defined targets. In advance of each trial, participants placed the stylus on a common start location (5-mm-radius white circle) in the middle of the display and maintained their visual gaze at this location for the duration of a trial. Following stylus placement, a 500-ms foreperiod was initiated after which one of four targets (5-mm-radius circle) appeared 140 (i.e., proximal target, ~17.3° visual angle) or 150 mm (i.e., distal target, ~18.4° visual angle) left or right of the start location. We selected the aforementioned eccentricities based on earlier work by our group, showing that such a range produces reliable between-target differences in planning-related cortical motor potentials (Krigolson et al. 2008, Krigolson et al. in press). Notably, the colour of the target provided participants with advanced knowledge regarding the nature of the to-be-completed response. A green target indicated a propointing response, whereas a red target indicated an anti-pointing response. Once the target had been projected for 1,000 ms, an auditory tone signalled participants to reach ‘quickly and accurately’. Importantly, the onset of reaching responses was delayed until after target presentation for two reasons. First, participants were required to withhold their responses for 1,000 ms after target presentation (i.e., when the auditory tone was provided) to equate pro- and anti-pointing for response suppression (Heath et al. 2009b, 2011; Olk and Kingstone 2003). Second, the paradigm provided an important methodological control preventing overlapping visual and motor ERPs.

Participants completed five blocks containing 80 trials each. Within each block, 10 trials were associated with each task (i.e., propointing and anti-pointing), reaching space (left space and right space) and target eccentricity (proximal target and distal target) combination. The ordering of individual trials was randomized within a block, and participants were provided self-paced rest periods between blocks.

Dependent variables and statistical analyses

Displacement of the stylus was filtered via a second-order dual-pass Butterworth filter using a low-pass cut-off

frequency of 10 Hz. Subsequently, instantaneous velocities were computed from displacement via a five-point central finite difference algorithm. Movement onset was defined as the first frame wherein velocity exceeded 30 mm/s for ten consecutive frames (80 ms). Movement offset was defined as the first frame in which velocity dropped below 30 mm/s for ten consecutive frames. Dependent variables included reaction time (RT, time from auditory initiation cue to movement onset), movement time (MT, time from movement onset to movement offset), and constant (CE) and variable (VE) error of reaching endpoints in the primary (i.e., horizontal) movement direction.

The EEG was recorded and pre-processed in a manner identical to Krigolson et al. (2008) with less than 7 % of the data discarded per participant. To analyse the visual response to the presentation of targets for pro- and anti-pointing, ERP waveforms were created by averaging epochs of the pre-processed data spanning from 200 ms before target onset to 600 ms after target onset from the continuous EEG data separately for each task and reaching space. We did not distinguish between the different target eccentricities in the EEG analysis due to the insufficient number of trials to analyse these data. Visual inspection of the ERP waveforms and a topographical analysis revealed two components of interest over parietal-occipital electrode sites PO7 and PO8. Specifically, we observed a N100 component, which has been shown to be sensitive to the focusing of spatial attention on a target location (Luck and Hillyard 1994), and a P300 component, which has previously been attributed to context-updating (Donchin and Coles 1988). For the purposes of statistical analysis, we quantified the N100 component using a base to peak measure between 150- and 250-ms post-target onset (Handy et al. 2001). To quantify the P300, we calculated the mean voltage between 350 and 450 ms following target onset (Krigolson et al. 2008). Both components were quantified for electrodes PO7 and PO8 separately for each participant as a function of task and reaching space.

Averaged behavioural data were examined via 2 (task: propointing and anti-pointing) by 2 (reaching space: left and right) by 2 (target eccentricity: proximal and distal) repeated measures ANOVA. Averaged ERP data were similarly examined with the exception that the variable target eccentricity was not included in the ANOVA model. An alpha level of 0.05 was used to interpret all statistical tests, and simple effects analyses were used to decompose interactions.

Results

The grand mean for RT was 283 ms (SD = 48), and no manipulation-related effects were associated with this

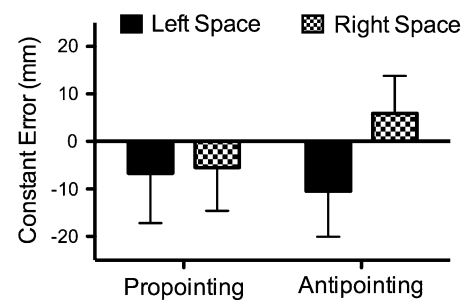


Fig. 1 Constant error (mm) in the primary movement direction for pro- and anti-pointing in left and right reaching space. Error bars represent one between-participant standard deviation

variable. Results for MT indicated that reaches to the proximal target (535 ms, SD = 38) produced shorter movement durations than reaches to the distal target (545 ms, SD = 40), $F(1,11) = 37.25$, $p < 0.001$. Results for CE revealed main effects for reaching space, $F(1,11) = 20.26$, $p < 0.01$, target eccentricity, $F(1,11) = 17.34$, $p < 0.01$, and a task by reaching space interaction, $F(1,11) = 19.47$, $p < 0.01$. Reaches to the proximal target (−2.5 mm, SD = 7.7) resulted in less undershooting than reaches to the distal target (−5.9 mm, SD = 13.4). In addition, Fig. 1 shows that propointing in left and right space exhibited an equivalent undershooting bias ($t(11) = 1.34$, $p = ns$), whereas anti-pointing in left and right space under- and overshoot veridical target location, respectively ($t(11) = 4.60$, $p < 0.01$). Last, VE for propointing trials (10.4 mm, SD = 2.0) was less than anti-pointing trials (12.5 mm, SD = 2.3), $F(1,11) = 21.90$, $p < 0.001$.

In line with previous accounts (Luck and Hillyard 1994), Fig. 2 shows that the N100 was maximal in the electrode contralateral to the presented target location for pro- and anti-pointing. Specifically, an electrode by reaching space interaction, $F(1,11) = 34.42$, $p < 0.001$, indicated that for targets presented in right reaching space, the N100 had a greater amplitude at electrode PO7 (7.2 μ V, SD = 3.1) than electrode PO8 (4.7 μ V, SD = 2.1) ($t(11) = 2.48$, $p < 0.02$). The converse relation was observed for targets presented in left reaching space (PO7: 4.9 μ V, SD = 2.5, PO8: 7.0 μ V, SD = 3.3) ($t(11) = -3.20$, $p < 0.01$). For conventional reasons, we have not outlined each null effect/interaction associated with this work. However, given our specific hypotheses regarding the N100, we thought it is important to document that this waveform did not reliably differ across pro- (5.93 μ V, SD = 3.11) and anti-pointing (5.98 μ V, SD = 2.93), $F(1,11) = 0.83$, $p = ns$.² For the P300, a main effect of task, $F(1,11) = 32.73$, $p < 0.001$, indicated a larger component for pro- (4.7 μ V, SD = 3.2) as compared to anti-pointing

² The magnitude of the F -ratio indicates that the null effect is not attributed to an inadequate replication sample size (Keppel 1991).

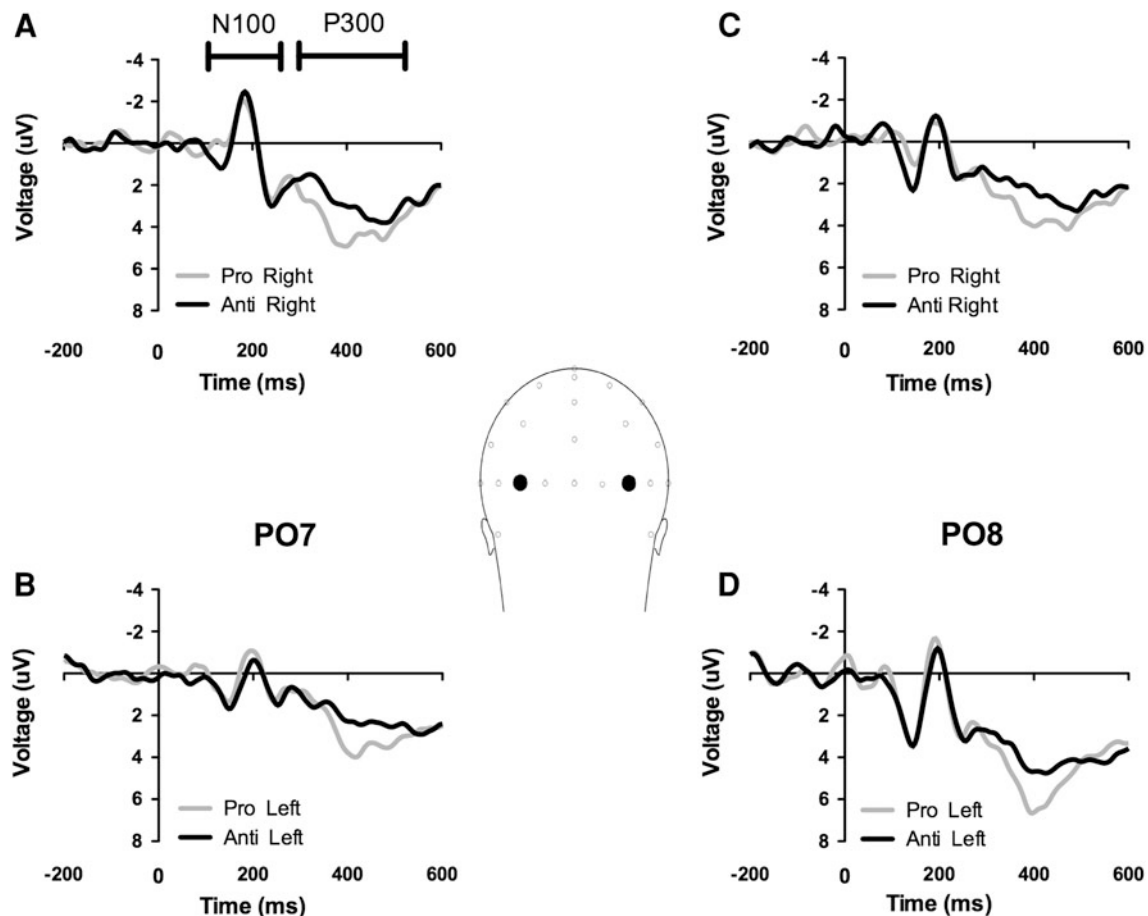


Fig. 2 Grand average event-related potential waveforms (μV) at parietal electrodes PO7 (*left side of head: a, b*) and PO8 (*right side of head: c, d*). The *upper and lower panels* represent PO7 and PO8 waveforms for pro- and antipointing when the target stimulus was presented in the *right and left visual fields*, respectively. From this

figure, it can be seen that the N100 component was larger in the electrode site contralateral to the target stimulus across pro- and antipointing. However, the later occurring P300 component reliably differed between pro- and antipointing across electrode sites

($3.3 \mu\text{V}$, $\text{SD} = 2.5$). Moreover, and as noted in Fig. 2, this difference was represented across electrodes PO7 and PO8.

Discussion

The present investigation contrasted the behavioural and ERP components of pro- and antipointing to test the competing predictions of the vector inversion and reallocation of attention hypotheses.

Behavioural measures of pro- and antipointing: response planning and endpoint bias

Pro- and antipointing produced equivalent reaction times. At the outset, this result appears contrary to the majority of studies demonstrating that ‘anti’ responses (i.e., antipointing and antisaccade) elicit longer reaction times than ‘pro’ responses (i.e., propointing and prosaccade). It is, however,

important to recognize that work reporting advantaged ‘pro’ reaction times have used a cuing paradigm wherein the sudden onset of a target serves as the response imperative (for antipointing see Heath et al. 2009a; for antisaccades see Hallett 1978). As a result, ‘pro’ responses are mediated via fast and stimulus-triggered visuomotor networks (so-called visual grasp reflex: see Pierrot-Deseilligny et al. 2005), whereas ‘anti’ responses require top-down, and time-consuming, suppression of the same networks. In the present investigation, the target stimulus was provided 1,000 ms in advance of response cuing; thus, a propointing reaction time advantage is not expected because this task required the same response suppression as antipointing. Moreover, that pro- and antipointing exhibited comparable reaction times indicate that vector inversion and/or the reallocation of attention necessary for antipointing was completed prior to response cuing (see below). These findings are consistent with neuroimaging work, showing that the constituent elements of a non-standard task are specified within the

first 500 ms of a delay interval (Van Der Werf et al. 2008). Additionally, the reaction time findings provide the present investigation with the timeline to contrast the ERP components of pro- and antipointing (i.e., prior to movement onset).

The results for endpoint accuracy showed that antipointing, but not propointing, produced a visual-field-specific endpoint bias such that left and right space reaches under- and overshoot veridical target location, respectively (Heath et al. 2009a, b; Maraj and Heath 2010). What is more, the absence of a between-task difference in reaction time indicates that response suppression is not related to the observed endpoint bias. After all, pro- and antipointing were equated for response suppression, and only the latter task demonstrated a visual-field-specific pattern of endpoint bias. We do, however, acknowledge that the visual-field-specific bias observed here may be limited by our use of two target eccentricities, that is, participants may have employed a cognitive label in reaching to a ‘near’ and a ‘far’ target. To address this issue, we collected supplemental behavioural data involving an additional ten participants (5 male and 5 female). We used the same methods as in the main experiment with the exception that a wider range of target eccentricities was employed (90, 110, 130, 150 and 170 mm). In line with our main experiment, results for CE produced a reliable task by reaching space interaction, $F(1,9) = 20.12$, $p < 0.01$, such that antipointing—but not propointing—exhibited a visual-field-specific pattern of endpoint bias. We propose that such results indicate that reaches were supported via target-specific direct and indirect (re)mapping processes. Moreover, the combined behavioural results from our main experiment and our supplemental data support the assertion that the inversion of target coordinates and/or a shift of attention renders perception-based processing of target features (i.e., extent) via relative—as opposed to absolute—visual metrics (Heath et al. 2009a, b; Maraj and Heath 2010). In the following section, we discuss our ERP findings in an effort to identify the extant process (vector inversion vs. reallocation of attention) associated with the visual-field-specific bias of antipointing.

Electrophysiological measures of pro- and antipointing: the N100 and the P300

Concerning the ERP data, ample work has shown that the N100 provides a sensitive metric for evaluating target-related attentional changes in perceptual and motor processing (Handy et al. 2001; Krigolson et al. 2008; Ritter et al. 1982). For example, Couperus (2010) found N100-related differences contralateral to a target stimulus when participants were required to distinguish between a target and a non-target item within a bilateral display. This

finding suggests that the N100 is sensitive to modulations of visuospatial attention across attended and unattended stimuli. As such, if antipointing is mediated by an obligatory ‘shift’ of visual attention from a target’s ‘pro’ to ‘anti’ coordinates than pro- and antipointing should be distinguishable by an overt difference in N100 amplitude or lateralization. As shown in Fig. 2, however, both pro- and antipointing elicited comparable N100 amplitudes, and for each task, the component was maximal in the parietal-occipital electrode contralateral to the target stimulus. In other words, antipointing (as well as propointing) was associated with enhanced focusing of early visuospatial attention on the target’s veridical location and not the mirror-symmetrical location associated with the ensuing reaching movement. Further, we note that our results are congruent with at least two studies examining the ERP components of the antisaccade task (Evdokimidis et al. 1996; Richards 2003). In particular, that work has shown that pro- and antisaccades produce comparable presaccadic ERP waveforms when information regarding the nature of the response (as was done here) is provided prior to response cuing. Thus, our results do not support Olk and Kingstone’s (2003) reallocation of attention hypothesis.

The P300 has been shown to relate to the revision of an internal model when a mismatch is detected between a stimulus and the required task goal (i.e., context-updating) (Donchin and Coles 1988; see also Nieuwenhuis et al. 2005). Moreover, in the motor domain, the P300 has been shown to precede trajectory amendments arising from an unexpected target jump, that is, the P300 has been related to an obligatory process of updating the spatial requirements of a movement goal (Krigolson et al. 2008). In the present study, we observed a reliable difference in the P300 of pro- and antipointing.³ We believe that this finding is important for at least two reasons. First, the timeline (i.e., ~350 ms following target onset) suggests that pro- and antipointing engaged in distinct visual processing of the movement environment prior to response cuing. This waveform difference coupled with the previously reported visual-field-specific endpoint bias of antipointing suggests that the P300 may be sensitive to the use of distinct visual metrics for pro- (i.e., absolute) and antipointing (i.e., relative). Second, we propose that the between-task difference in the P300 supports the vector inversion hypothesis. In particular, we propose that the waveform difference indicates that antipointing is associated with the process of remapping (i.e., context-updating) a target’s veridical

³ The P300 is normally measured along midline site Pz where it is maximal. In the present study, we elected to report the P300 at PO7 and PO8 to facilitate comparisons with the N100. Importantly, however, the P300 difference noted between pro- and antipointing at PO7 and PO8 was similarly reflected at Pz ($p < 0.001$).

location to a mirror-symmetrical location in reaching space.

We recognize that our findings differ from a frequently cited study examining the EEG correlates of antisaccades (Everling et al. 1998; see also Moon et al. 2007). In that work, a shift of negative potentials was observed in a parietal electrode site contralateral to the target to a homologous site ipsilateral to the target: a pattern interpreted as strong support for the vector inversion hypothesis. In contrast, the present study found that P300 differences were represented bilaterally. In reconciling this finding, we note that although antipointing and antisaccades require vector inversion, only the former task requires the additional transformation of ‘anti’ coordinates into an appropriate hand-centred frame of reference (Flanders et al. 1992). Accordingly, the specification of target location via a hand-centred frame of reference (as opposed to the retinocentric frame for antisaccades) may result in antipointing recruiting more diffuse neural generators (see also Connolly et al. 2000).

In summary, our EEG data provide evidence that antipointing is mediated via a process of visual vector inversion. Moreover, the EEG data combined with the visual-field-specific endpoint bias of antipointing indicates that the top-down nature of vector inversion engenders a perception-based representation of target extent.

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