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Research Report

Electrophysiological evidence for a post-perceptual influence of global visual context on perceived orientation

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ABSTRACT

Visual orientation cues largely determine our perceptions of “vertical,” as illustrated in the Rod and Frame Illusion (RFI): an upright rod appears slanted in the opposite direction of a surrounding tilted frame. We used event-related potentials (ERPs) to examine the cortical time course of the frame’s illusory influence on the perceived orientation of the rod. ERPs to an orientation discrimination task revealed: 1) the amplitudes of the P1 and N1 (indices of early visual processing) were not affected by frame tilt, but the amplitude of the P3 (an index of later processing) was, and 2) increasing the perceptual difficulty of the rod tilt judgment did not affect the P1 or N1, but increased response time and attenuated P3 amplitude. Results suggest that global orientation context effects are manifest during later, post-perceptual stages of information processing.

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1. Introduction

The perceived orientation of any given edge in our visual field is influenced by many factors, including the processes of our vestibular system, proprioception, and vision. One of the most influential cues governing our perception of vertical, or upright, comes from the larger visual environment surrounding the edge in question. These surrounding edges can readily lead us to misperceive the orientation of a target edge. The Rod and Frame Illusion (RFI) illustrated in Fig. 1 provides a basic demonstration of how such misperceptions can occur. The orientation of the rod appears tilted in the opposite direction of the surrounding square frame (e.g. Asch and Witkin, 1948), with peak effects when the frame is tilted approximately 15° from gravity-defined vertical (0°) (Beh et al., 1971; Wenderoth and Beh, 1977). While such misperceptions can be hilarious, they could also be deadly. On the one hand, these tilt effects underlie the phenomena experienced at popular tourist

attractions such as “Mystery Cabins.” Visitors can witness objects and people balancing in gravity-defying postures as a direct consequence of the slanted walls, floor, and ceiling of the tilted cabin. On the other hand, these tilt illusions can also occur in critical safety situations that call for accurate orientation perception within milliseconds, such as when a pilot must quickly determine the orientation of an approaching runway in a landing field. Therefore, an understanding of the time course and neural locus of orientation context effects is of particular importance.

1.1. When are global orientation context effects manifest?

While the spatial parameters of the RFI and related global orientation context illusions have been well catalogued, an understanding of the time course of these tilt effects is overdue. In the present investigation, we took advantage of the temporal precision afforded by event-related potential

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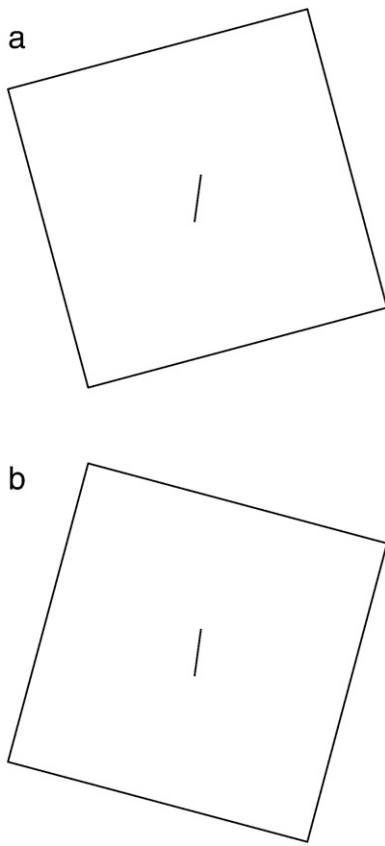


Fig. 1 – Examples of a) incongruent and b) congruent trials. Observers determined whether the rod was tilted CCW (left) or CW (right) from gravitational vertical (in this example, “CW” (right) was the correct response). Although the two rods are physically identical, the perceived orientation of the rod is biased in the opposite direction of the frame, such that the rod in panel (a) surrounded by an incongruently tilted frame appears more tilted from gravitational upright than the rod in panel (b) surrounded by a congruently tilted frame.

(ERP) methodology, in conjunction with behavioral measures, to examine the cortical time course of the RFI. Averaging ERP signals over many experimental trials allowed us to measure a more precise and continuous estimate of the cortical activity between the onset of the rod and the observer’s response to a rod orientation discrimination task, without the added time required to plan and execute behavioral responses. Specifically, we examined the cortical contributions of early processing (e.g. stimulus identification) and later, post-perceptual processing (e.g. response selection) to global orientation context illusions such as the RFI (see Vogel et al., 1998 for a similar approach). Before describing our experiments, we will briefly review the literature regarding: 1) the global nature of the RFI, 2) the time course of global orientation context illusions, and 3) the ERP components of interest in the present investigation.

1.1.1. The global nature of the RFI

RFI displays are usually composed of large inducing frames and small test rods, with large retinal separations between the rod and frame (e. g. Dyde and Milner, 2002; Asch and Witkin, 1948). Such a large separation between edges in itself demonstrates a

long-range or global context effect (Beh et al., 1971). However, two other findings emphasize this even more: 1) increasing the retinal size of the frame increases its bias on the perceived orientation of the rod (Ebenholtz, 1977; Ebenholtz and Callan, 1980), and 2) the orientation of the rod is ultimately perceived relative to the most global frame of reference. For example, an upright rod appears tilted when surrounded by a small upright frame and a large tilted frame, but the same rod appears upright when surrounded by a small tilted frame and a large upright frame (Spinelli et al., 1995; DiLorenzo and Rock, 1982). Recently Daini and Wenderoth (2008) reported that when two frames are used, the orientation of the inner frame is biased by the orientation of the outer frame, which in turn biases the orientation of the central rod, such that orientation bias is induced sequentially from the most global to the innermost stimulus. Overall, the RFI and related illusions result from mechanisms that take into account the relative orientation of edges within a hierarchically organized surrounding environment.

1.1.2. The time course of global orientation perception

The well-established orientation selectivity of neurons in the striate area of visual cortex (Hubel and Wiesel, 1962) underlies the widely accepted proposal that edge orientation is a fundamental or primitive feature contributing to all subsequent visual processing (e.g. Adams et al., 2007; Cheng et al., 2001; Haynes and Rees, 2005). Sometimes these early and spatially local processes provide an adequate account of orientation effects in perceptual experience, as seems to be the case in the tilt illusion (TI), where the orientation of a central grating is biased by the orientation of an immediately adjacent neighboring grating (Wenderoth and Smith, 1999). However, once the contextual stimulus edges are spatially removed from the immediate neighborhood of the central stimulus, as occurs in the RFI, the spatially local effects of neurons in striate cortex are no longer adequate. To account for these longer-range effects, Wenderoth and Johnstone (1987) have speculated that the RFI is mediated by total receptive field responses of orientation-tuned neurons in later extrastriate areas. In support of this proposal, we recently examined the time course of the RFI psychophysically, reporting findings that were consistent with a relatively late influence of the surrounding frame on the perceived orientation of the central rod (Corbett et al., 2009). Furthermore, a recent fMRI investigation has demonstrated activation in later dorsal parietal areas specific to the mislocalization of a target presented slightly offset from midline or “straight ahead,” which appears shifted in the opposite direction of a surrounding offset frame (Roelofs’ Effect) (Walter and Dassonville, 2008).

Support for a relatively late neural locus comes from Dyde and Milner (2002), who reported that when observers misperceived the position of a rod inside a tilted frame, they could still make accurate visually guided posting and grasping actions to the rod. These authors contend that the absence of a visuomotor illusion is evidence that the RFI does not affect dorsal visuomotor mechanisms, but occurs in ventral brain areas downstream, after the bifurcation of the ventral and dorsal visual streams carrying information for perception and visually guided action, respectively (Milner and Goodale, 1995). Specifically, they propose that the RFI “operates late within the ventral stream...where perceptions are constructed with global reference to the wider visual environment (Dyde and Milner, 2002, p. 526).”

Also consistent with a later locus for global orientation cues, Li and Matin (2005) reported that the accuracy of manual pointing and reaching actions to a dot flanked by a large, pitched-from-vertical line increased as the distance from the hand-to-body increased. Actions were initially mislocalized to a similar degree as the illusory perception of eye level induced by the tilted line, but terminated in accordance with the physical position of the dot. Li and Matin propose that these results reflect a greater weighting of internalized, observer-based, proximal orientation cues during the initial stages of manual actions, transitioning to a greater weighting of distal, or environmental-based orientation cues as the distance from the hand-to-body increases. Taken together, these studies suggest that the RFI occurs late in the course of orientation perception, at least after response planning and initiation.

1.1.3. ERP components of interest to the present investigation
 Since we are primarily concerned with whether global orientation context effects are manifest before or after the initial identification of the stimulus, we chose to examine three predominant ERP components, the P1, N1, and P3. These components occur well within an 800 ms period between the onset of the RFI stimulus and the observer's response to a rod orientation discrimination task, and they are generally agreed upon as markers of "perceptual" and "post-perceptual" processes. The terms perceptual and post-perceptual are commonly used in the ERP literature to distinguish between effects that occur before and after a stimulus has been identified, respectively (e.g. Vogel et al., 1998). This does not necessarily mean that the stimulus is not perceived as having the effect of interest, just that the effect is manifest after the stimulus has been identified. For example, in the present case, the rod could appear tilted because it is processed as part of a larger compound stimulus, composed of both the rod and frame (an early, perceptual effect), or that the perceived tilt of the rod is biased only after it has been related to the tilt of the surrounding frame (a later, post-perceptual effect). The question here, then, concerns *when* the reference to the wider environment of the tilted frame influences the perceived tilt of the rod; that is, whether it occurs *before* or *after* the rod stimulus is initially identified as an object distinct from its background.

1.1.3.1. Perceptual markers. Neural activity associated with early, sensory and perceptual-level visual processing, such as detection, discrimination, and the deployment of spatial attention, is indexed by an increase in the amplitude of the P1 component (the first positive deflection typically observed in visual ERP waveforms 100 ms after stimulus onset), and/or N1 components (the first negative deflection typically observed 200 ms after stimulus onset). Both of these components are largest over occipital scalp areas (Luck and Hillyard, 1995; Heinze et al., 1994; Woldorff et al., 1997; Mangun and Hillyard, 1991).¹

¹ It should also be noted that although ERPs provide a precise estimate of the time course of cortical activity relative to the presentation of a stimulus, the precise neurological structures responsible for the generation of canonical ERP waveform components such as the P1, N1, and P3 remain to be determined. As such, ERPs are very poor tools for spatial localization (see Handy, 2005 for a review).

1.1.3.2. A post-perceptual marker. Changes in the amplitude of the P3 component, or the third positive-going deflection in visual ERP waveforms over midline parietal/central scalp regions 300 ms after stimulus onset are associated with post-perceptual processing. Specifically, the amplitude of the P3 is inversely related to the probability of the category to which the stimulus belongs occurring in the specific task at hand (see Johnson, 1986 for a review). For example, in a letter/number categorization task, if numbers are presented less frequently than letters, a less frequent or "oddball" number "3" will elicit a larger amplitude P3 than the more frequent and therefore more expected letter "E." The leading hypothesis is that P3 amplitude reflects a contextual updating of working memory, after the stimulus has been categorized, with larger P3 amplitude for stimuli that are out of context, less probable, or less expected (Donchin and Coles, 1988).²

Stimulus orientation has been reported to affect both perceptual and post-perceptual ERP components, sometimes even in the same study. For example, when subjects were adapted to a tilted grating and then briefly presented with a vertical test grating, early Visual Evoked Potential (VEP) activity approximately 100 ms after the presentation of the test stimulus became more positive as the orientation of the adapting grating was increased from 0° to 60° (Smith and Jeffreys, 1978). On the other hand, when a display of randomly oriented line elements gradually came together to form a "Gestalt" grid and then gradually moved apart, the later P3 component was larger over dorsal parietal areas when the grid was oriented 45° than when it was upright, or when the elements did not form a recognizable pattern (Heinrich et al., 2008). Results from a recent ERP investigation using binocular rivalry to investigate the cortical time course of awareness suggest that both early and late stages of processing are modulated by stimulus orientation. Roeber et al. (2008) presented observers with a +45° Gabor in one eye and a -45° Gabor in the other eye. This induced binocular rivalry such that only one Gabor was consciously perceived at a time. Observers held down a key to indicate which of the two stimuli they currently perceived. When the visible Gabor changed in orientation to match the non-visible Gabor, observers were aware of the change and the amplitudes of the P1, N1, and P3 were larger than in the physically identical situation when the non-visible Gabor changed in orientation to match the visible Gabor and observers were not aware of the change. Overall, these results do not allow for a clear prediction of when global orientation context effects are manifest, as they suggest both perceptual and post-perceptual components are sensitive to orientation discriminations.

1.2. The present study

The present study was conducted to examine whether the perceived orientation of a stimulus is affected by the context

² Two distinct components of the P3 have now been identified (see Soltani and Knight, 2000 for a review). In this investigation, we are concerned with the P3b, hereafter referred to as the P3. The other component, the P3a, is mainly evoked over frontal areas and the insula by distractors (Soltani and Knight, 2000; Bledowski et al., 2004), which were not present in our displays.

of the wider visual environment, outside the scope of spatially local receptive fields in striate cortex believed to underlie local tilt effects such as the TI. Here we use a variant of the traditional RFI task, in which participants determined the orientation of a slightly tilted rod appearing in the center of a congruently or incongruently tilted frame. We first measured the effects of frame orientation on the perceptual P1 and N1 components, and the post-perceptual P3 component. To anticipate the results of Experiment 1, the orientation of the frame modulated the amplitude of the P3, but the P1 and N1 components were unaffected. In Experiment 2, we tested whether increasing the perceptual difficulty of the RFI task might increase any latent P1 or N1 effects undiscovered by the easier discrimination in Experiment 1. This idea was inspired by earlier reports that P1 and N1 attention effects may require relatively higher levels of perceptual load (Handy and Mangun, 2000). We manipulated difficulty by inducing head tilt, which increases the difficulty of orientation discrimination (e.g. Corbett and Enns, 2006). These results confirmed evidence for late, but not early, effects of the inducing frame on rod orientation judgments.

2. Experiment 1

In Experiment 1, observers discriminated as rapidly as possible whether the target rod presented inside the tilted frame was oriented Counterclockwise (CCW) or Clockwise (CW) from gravitational upright. Similar to the methods of Roeber et al. (2008), we used a version of the illusion in which a tilted frame could induce two different percepts of a physically identical stimulus: one that aids discrimination of the rod's physical tilt, and one that impairs rod orientation discrimination. When the rod and frame are incongruently oriented (Fig. 1a), the mismatch in orientation accentuates the tilt of the rod, making it appear even more tilted from upright than it physically is. On the other hand, when the rod and frame are tilted congruently, the orientation of the rod is biased in the opposite direction of the tilted frame causing the rod to appear less tilted, upright, or even slightly tilted in the opposite direction (Fig. 1b).

To examine the time course of the illusion as closely and as sensitively as possible, we chose not to measure the traditional Point of Subjective Vertical (PSV), or the magnitude of the illusion at a given time-point. Instead, we measured the time it took participants to correctly discriminate whether the rod was oriented CCW or CW. The traditional PSV measure allows for an interpretation of the effects of the inducing context on the subjective percept of orientation only after visual processing is complete. Here our measurement of response time and accuracy indexes performance-based influences of the contextual frame during ongoing processes that may not be reflected in the final conscious perception of the rod's tilt. Importantly, as we were interested in the temporal dynamics of global orientation context effects, measuring response time and accuracy allowed for a more sensitive and appropriate time-based measure, as compared to a space-based PSV measure.

In conjunction with behavioral measures, we recorded ERPs elicited by the rod tilt discrimination as a function of the

orientation of the frame. As outlined above, modulations of the amplitude of earlier P1 and/or N1 components would suggest that the RFI influences early levels of visual processing. Conversely, differences in the amplitude of the P3 component would provide electrophysiological support for a late temporal locus of global tilt illusions such as the RFI.

2.1. Results

2.1.1. Behavioral RFI criterion

As some observers are less dependent on the orientation of the surrounding visual field to determine upright (e.g. Witkin, 1949), we used a behavioral criterion to distinguish observers who were subject to the RFI. We collapsed the data over CCW and CW rod tilts to compare incongruent trials to congruent trials. For incongruent trials, observers should respond faster if the rod appears more tilted than it physically is (Fig. 1a). For congruent trials, they should respond slower if the rod looks less tilted or even tilted in the opposite direction (Fig. 1b). Thirty-seven of the forty-one participants met our behavioral criterion such that they correctly responded faster to incongruent trials relative to congruent trials, $t(36)=8.52$, $p<.001$ (Fig. 2). The same pattern held for response accuracy, such that observers responded with higher average levels of accuracy in incongruent trials as compared to congruent trials, $t(36)=5.48$, $p<.001$. Because we required participants to achieve an average accuracy of at least 85% in order to proceed to the experimental trials, we did not analyze their accuracy in any greater detail.

2.1.2. Electrophysiological data

We collapsed the resultant ERPs for correct trials across CCW and CW rod tilts, and then used participants' averaged waveforms to derive the grand-averaged waveforms for incongruent and congruent trials. We analyzed the mean amplitudes of the P1, N1, and P3 components in the grand-averaged ERPs by computing mean amplitudes for each component relative to a 200 ms pre-stimulus baseline, and then identifying the latency of the peak amplitude of each waveform for each electrode and condition of interest. Specifically, we compared incongruent and congruent ERPs over lateral and central occipital electrode sites T₅, T₆, O₁, O_z, and O₂ (scalp locations where the P1 and N1 are maximal), and

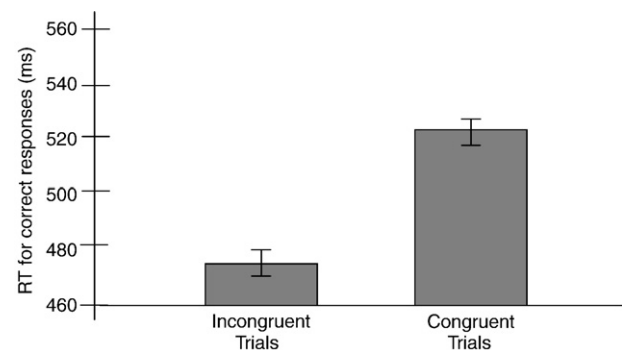


Fig. 2 – Mean correct response times to incongruent and congruent trials for participants who were subject RFI in Experiment 1. Error bars indicate ± 1 SEM.

over midline parietal sites C_z and P_z (scalp locations where the P3 is maximal) (Coles and Rugg, 1995). For data points entered into the following statistical analyses, we then measured the amplitude of the single-subject waveforms within each electrode and condition during the 20 ms window surrounding the corresponding peak amplitude for each component in the grand average (see Handy, 2005). For observers considered in ERP analyses, no more than 10% of trials were rejected due to artifacts in each of the four conditions resulting from all possible combinations of the two rod positions (CCW and CW), and the two frame positions (CCW and CW).

In the grand-averaged waveforms, the P1 was maximal approximately 100 ms to 120 ms after the onset of the rod, and the N1 was maximal approximately 180 ms to 200 ms, both over lateral occipital electrode sites, T_5 , T_6 , O_1 , O_z , and O_2 . The P3 was maximal approximately 390 ms to 410 ms after the onset of the rod over midline parietal sites C_z and P_z . Observers who were subject to the RFI showed no significant effects of Frame Tilt on the mean peak amplitudes of the P1, or the N1 in repeated-measures ANOVAs (F 's < 1, p 's > .52). In contrast to these null results for early components, a single-factor repeated-measures ANOVA on the mean peak P3 amplitudes showed an increase in the amplitude of the P3 component for incongruent frame trials relative to congruent frame trials, $F(1,36)=25.81$, $p < .001$ (Fig. 3). While the rod tilt discrimination elicited P1, N1, and P3 components in all observers, the same analyses for the four of forty-one observers who were not subject to the RFI showed no modulation of any of these components in individual or grand-averaged waveforms. Finally, a correlational analysis of all forty-one participants in Experiment 1 confirmed a significant negative relationship between the difference in RT for congruent–incongruent trials and the P3 amplitude difference for congruent–incongruent trials, $r = -.325$, $p = .05$.

2.2. Discussion

The results of Experiment 1 are consistent with a later, post-perceptual locus for the RFI. Over all forty-one participants, the greater the effect of Frame Tilt on manual RT, the larger was its effect on P3 amplitude. The majority of observers showed behavioral RFI effects, as indicated by a main effect of Frame Tilt, such that rod tilt discriminations in incongruent trials were significantly faster than congruent trials. These observers also showed a corresponding effect of Frame Tilt on the mean peak amplitude of the P3. Specifically, the orientation of the surrounding frame modulated the amplitude of the P3 signal, with larger P3 amplitudes for incongruent trials relative to congruent trials. In contrast, the few observers who did not show behavioral evidence of the RFI also showed no evidence of an effect of Frame Tilt on the amplitude of the P3. In addition, while the orientation discrimination task elicited P1 and N1 components as expected, the lack of a significant effect of Frame Tilt on these components for all observers provided no evidence that the RFI was manifest during early sensory and perceptual processing. As the P3 has been linked to post-perceptual processes, such as response categorization, our findings imply that the bias in perceived vertical induced by the tilted frame occurs during these later stages of processing.

3. Experiment 2

We conducted Experiment 2 in consideration of the possibility that the rod tilt discrimination task in Experiment 1 was not demanding enough to detect an effect of the frame on the earlier P1 and N1 components. Handy and Mangun (2000) reported that detecting P1 and N1 attention effects can require relatively high levels of perceptual load. In Experiment 2, we increased the difficulty of our task by manipulating head tilt. Viewing the RFI display with a tilted head increases the difficulty of orientation discrimination in the same way that vestibular and proprioceptive damage or Galvanic Vestibular Stimulation (GVS) increase its difficulty (Corbett and Enns, 2006; Bischof, 1974; Guerraz et al., 1998; Merker and Held, 1981; Young et al., 1975; Allison et al., 1999; Kennedy et al., 2003; Vibert et al., 1999; Guerraz et al., 2001; Hafstrom et al., 2004; Lopez et al., 2006; Yardley, 1990). Here we hypothesized that head tilt would increase the difficulty of the rod tilt discrimination task, as indexed behaviorally by an increase in correct response times and a coinciding decrease in the amplitude of the P3 elicited by the rod tilt judgment. We readily acknowledge that many potential mechanisms may contribute to the increase in difficulty that accompanies head tilt (e.g., visual, vestibular, proprioceptive, and egocentric processes). For our purposes here, it is only important that head tilt increases behavioral difficulty so that we are able to 1) better detect P1 and N1 effects if they exist, and 2) disentangle the magnitude of the illusion (congruent–incongruent response time) from the overall difficulty of making the discrimination (mean response time).

3.1. Results

Nineteen of the twenty-two observers met the behavioral response time criterion for experiencing the RFI, such that when their heads were upright and they were viewing a tilted frame, they correctly responded faster to incongruent rods versus congruent rods. For each of these observers, no more than 10% of trials were rejected due to artifacts in each of the eight conditions resulting from all possible combinations of the two head positions (upright and tilted), the two rod positions (CCW and CW), and the two frame positions (CCW and CW).

3.1.1. Behavioral data

The nineteen observers who were subject to the RFI when their heads were upright were also subject to the illusion when their heads were tilted (Fig. 4). Head tilt and congruent frame tilt slowed correct responses, as confirmed by a 2×2 repeated-measures ANOVA, which revealed significant main effects of Head Tilt (Upright, Tilted), $F(1,18)=20.17$, $p < .001$, and Frame Tilt (Incongruent, Congruent), $F(1,18)=39.00$, $p < .001$, but no interaction of Head Tilt \times Frame Tilt, $F(1,18) < 1$.

3.1.2. Electrophysiological data

Fig. 5 shows the ERPs in each condition (Head Upright and Tilted) for the nineteen observers in Experiment 2 who demonstrated a behavioral RFI. We first conducted repeated-measures ANOVAs on the amplitudes of the P1 (100–120 ms) and the N1 (180–200 ms) over lateral occipital electrode sites,

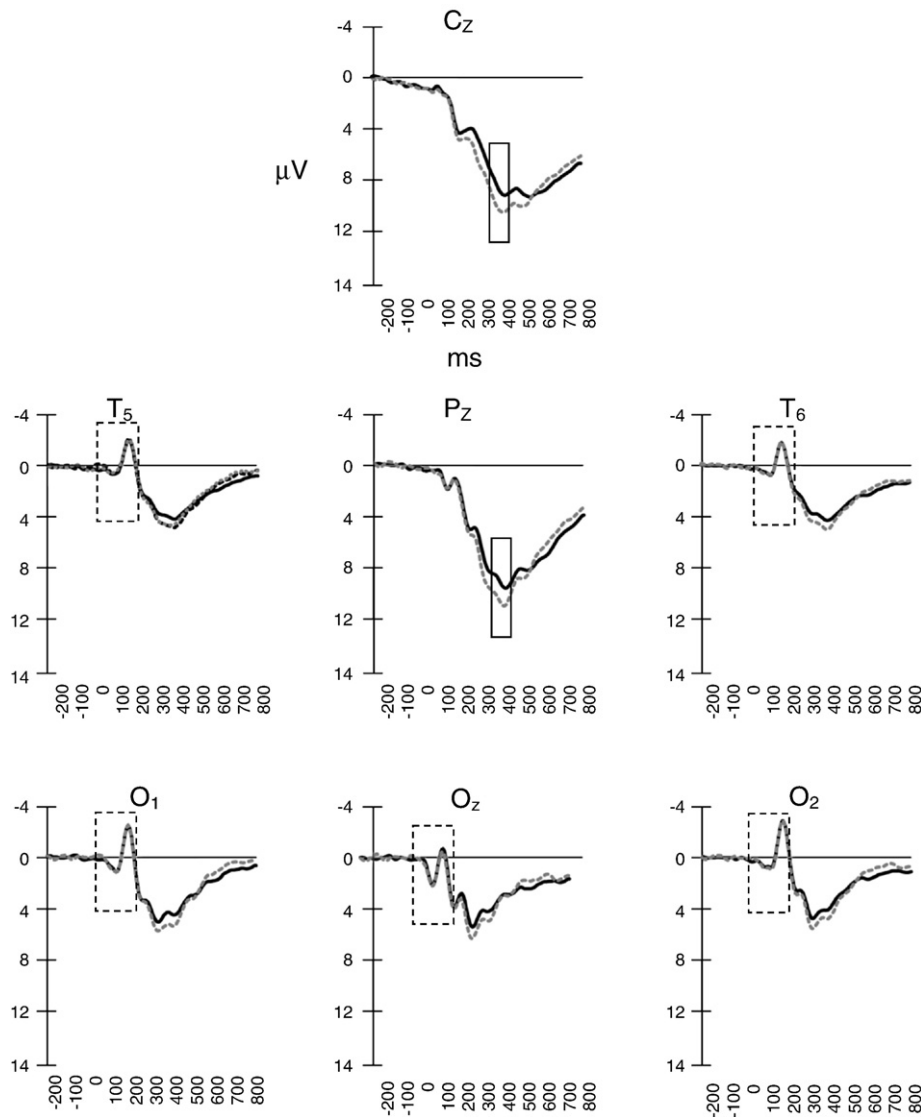


Fig. 3 – Grand-average ERP waveforms at lateral occipital and midline parietal electrode sites for incongruent trials (dashed line) and congruent trials (solid line) in Experiment 1. The modulations of the P3 amplitude over midline parietal electrode sites C_z and P_z are outlined with solid rectangles, and the lack of corresponding effects in P1 and N1 amplitudes over lateral occipital sites T_5 , T_6 , O_1 , O_z , and O_2 are outlined with dashed rectangles.

T_5 , T_6 , O_1 , O_z , and O_2 and found no significant effects of Frame Tilt or Head Tilt (F 's < 1, p 's > .412). We next conducted an omnibus ANOVA to concurrently examine the P3s in each condition. Since head tilt increased correct response times, we wondered whether it also affected the time course of the P3. To examine this we included Time Window as a factor in our initial omnibus analysis of the P3. Specifically, we compared the effects of Frame Tilt (Incongruent, Congruent), Time Window (250–300 ms, 300–350 ms, 350–400 ms, and 400–450 ms), and Head Tilt (Upright, Tilted) on the mean amplitudes at electrode sites C_z and P_z .

Observers who were subject to the behavioral RFI showed a larger amplitude P3 elicited by the rod tilt discrimination over midline parietal sites C_z and P_z for incongruent rod and frame trials compared to congruent rod and frame trials, as indicated by a main effect of Frame Tilt, $F(1,18)=11.90$, $p<.005$. Overall, Head Tilt marginally attenuated the amplitude of the P3, F

(1,18)=3.97, $p=.06$. In addition, we found a main effect of Time Window, $F(3,54)=39.02$, $p<.001$, and interactions between Time Window and Frame Tilt, $F(3,54)=3.91$, $p<.05$, and Time Window and Head Tilt $F(3,54)=3.06$, $p<.05$.

To confirm the interpretations drawn from our omnibus ANOVA, we performed separate 2 (Head Tilt) × 2 (Frame Tilt) repeated-measures ANOVAs within each time window. We found a main effect of Frame Tilt with a decreased P3 for congruent relative to incongruent frame tilts at each of the four consecutive time windows (all F 's > 4.76, all p 's < .05). We also found a significant main effect of Head Tilt, with a decreased P3 amplitude when observers' heads were tilted compared to when they were upright in the 300–350 ms time window, $F=4.44$, $p<.05$, and the 350–400 ms time window, $F=7.88$, $p<.02$. Finally, the factors of Head Tilt and Frame Tilt interacted significantly in the 300–350 ms time window, $F=4.75$, $p<.05$, illustrated by the decreased P3 for incongruent

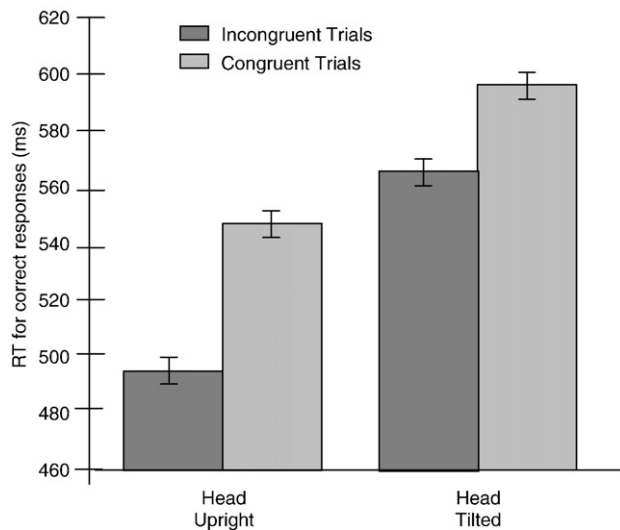


Fig. 4 – Mean correct response times to incongruent and congruent trials for participants who were subject RFI in the Head Upright and Head Tilted conditions of Experiment 2. Error bars indicate ± 1 SEM.

frame trials when the head was tilted relative to the P3 for incongruent frame trials when the head was upright (Fig. 5). As in Experiment 1, no modulations of any components were observed for the three participants in Experiment 2 who were not subject to the RFI. Finally, a correlational analysis of all twenty-two participants in Experiment 2 showed, as in Experiment 1, that the difference between congruent and incongruent RTs was inversely related to the difference between congruent and incongruent P3 amplitudes, both when the head was upright ($r = -.483$, $p < .05$), and when it was tilted ($r = -.425$, $p < .05$).

3.2. Discussion

The ERP effects we observed for participants in Experiment 2 were again consistent with their patterns of correct speeded response across the eight combinations of Head Tilt (2) and Time Window (4). As in Experiment 1, the nineteen participants in Experiment 2 who exhibited a behavioral RFI did not exhibit any differences in their early P1 or N1 components. Also, as in Experiment 1, for participants with a behavioral RFI, correct response times increased and P3 amplitudes decreased for congruent versus incongruent trials, and when the head was upright versus tilted. Specifically, Head Tilt attenuated the amplitude of the P3 at the 300–350 ms and 350–400 ms time windows, and interacted with Frame Tilt to decrease the P3 amplitude in incongruent frame trials at the 300–350 ms time window.³ Finally, as in Experiment 1, the three observers who did not show behavioral evidence of the

³ We did not analyze more acute time windows, and we note that our choice of 50 ms intervals may have “clipped” the effects Head Tilt or the interaction between Head Tilt and Frame Tilt that may have emerged with more precise intervals. However, our purpose for this analysis was simply to demonstrate that Head Tilt affected the amplitude of the P3 concomitantly with behavioral reaction times.

RFI showed no evidence of an effect of Frame Tilt on the amplitude of the P3.

Our findings agree with earlier behavioral reports that head tilt impairs the ability to determine upright in the presence of the RFI and other orientation illusions (Corbett and Enns, 2006; Bischof, 1974; Guerraz et al., 1998; Merker and Held, 1981; Young et al., 1975; Allison et al., 1999). The results concerning head tilt in Experiment 2 are also consistent with the increased difficulty in perceiving vertical, or upright, that results when the vestibular organs are directly stimulated via GVS (Kennedy et al., 2003), and to the increased magnitude of the RFI exhibited by patients with vestibular and proprioceptive disorders (Vibert et al., 1999; Guerraz et al., 2001; Hafstrom et al., 2004; Lopez et al., 2006; Yardley, 1990). Importantly, contrary to findings by Handy and Mangun (2000) that P1 and N1 attention effects require higher levels of difficulty, increasing the perceptual difficulty of our rod tilt discrimination task did not affect the amplitude of the P1 or N1 components, but did affect the P3 component. In addition, subjects who exhibited a behavioral RFI in both Experiments 1 and 2 did not demonstrate any effects in early P1 or N1 components. Therefore, we interpret the observed decrease in P3 amplitude to reflect a more difficult categorization of the rod's tilt when the head is also tilted from upright, and the lack of effects on the P1 and N1 as reflecting a lack of RFI effects during early sensory and perceptual stages of processing. Overall, the results of Experiment 2 provide further evidence that the RFI is manifest during post-perceptual stages of processing, after earlier stimulus encoding and identification stages.

4. General discussion

This study provides the first electrophysiological evidence that global orientation context effects are manifest during relatively late stages of processing. In Experiment 1, we found that the amplitude of the P3 component was larger when the rod and frame were tilted incongruently versus congruently, but that the orientation of the frame did not affect earlier P1 and N1 components. Contrary to findings that higher levels of perceptual difficulty are necessary to elicit P1 and N1 attention effects (Handy and Mangun, 2000), the harder rod tilt judgment in Experiment 2 when observers' heads were tilted still did not affect these earlier components. Head tilt did increase correct response times and attenuate the amplitude of P3's in response to rod tilt discriminations. These results are consistent with reports that head tilt, direct vestibular stimulation, and vestibular/proprioceptive disorders increase the difficulty of orientation discriminations (Corbett and Enns, 2006; Bischof, 1974; Guerraz et al., 1998; Merker and Held, 1981; Young et al., 1975; Allison et al., 1999; Kennedy et al., 2003; Vibert et al., 1999; Guerraz et al., 2001; Hafstrom et al., 2004; Lopez et al., 2006). We therefore interpret the observed P3 effects in both experiments to reflect a post-perceptual effect of the frame's global context on the perceived orientation of the rod.

4.1. Limitations of the present study

ERPs provide only an upper bound for the locus of the global context effects under investigation in the present study, as

cortical activity recorded at the scalp reflects only a small portion of underlying neural activity. Given this limitation, it is possible that our recordings were not sensitive enough to detect modulations of the earlier P1 and N1 components, even under increased levels of perceptual load previously demonstrated to evoke P1 and N1 attention effects (Handy and Mangun, 2000). Nevertheless, the P3 we obtained in response to rod tilt judgments was modulated by the orientation of the frame, as well as the increased difficulty of rod tilt judgment imposed by head tilt (e.g. Corbett and Enns, 2006; Young et al., 1975). Regardless of whether our measures were sensitive enough to detect earlier effects, we did find a post-perceptual influence of the global orientation context of the frame, in accordance with earlier behavioral findings suggesting a later involvement of global mechanisms in interpreting the orientation of the wider visual environment (e.g. Dyde and Milner, 2002; Li and Matin, 2005). Therefore, while the present results provide

strong support for the proposal that the RFI is manifest during later stages of processing, further investigation mapping the neural substrates of the illusion is necessary to confirm predictions that global orientation constancy mechanisms are mediated later extrastriate areas (e.g. Wenderoth and Johnstone, 1987).

In addition, we note that humans must continuously reference multiple visible orientation cues and non-retinal vestibular and proprioceptive inputs to prevent disorientation with each slight change of viewpoint. Admittedly, the present study captures only one small slice of time, with brief exposures to a sparse tilted context. Future work will also have to be directed at the on-line integration of available visual orientation signals over time.

Finally, ocular torsion (compensatory eye movements due to the incorporation of non-retinal vestibular inputs during head tilt) may play a role in the increased difficulty indexed by response times and P3 amplitudes in the head

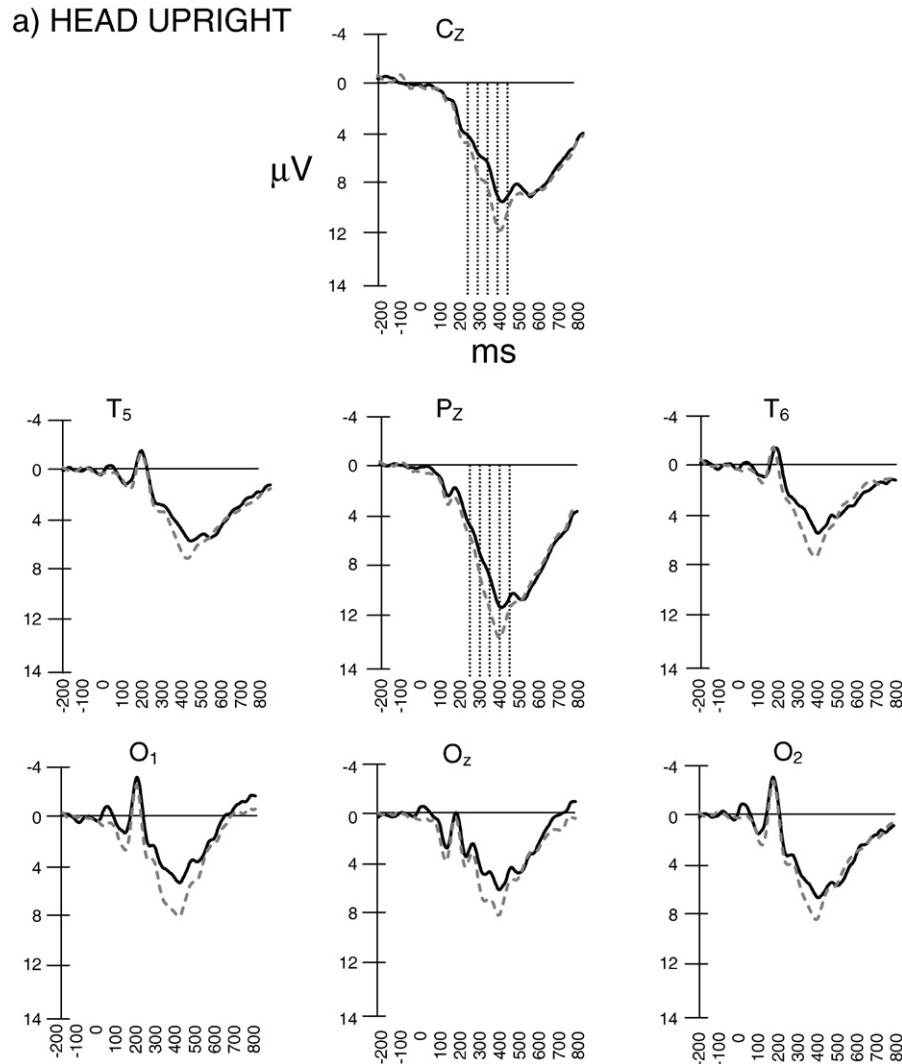


Fig. 5 – Grand-average ERP waveforms for incongruent trials (dashed line) and congruent trials (solid line) in Experiment 2 in the a) Head Upright condition (top), and the b) Head Tilted condition (bottom) for P3 midline parietal electrode sites C_z and P_z , and P1/N1 lateral occipital sites T_5 , T_6 , O_1 , O_z , and O_2 . Perforations indicate the four consecutive time windows used in the analysis of the P3 amplitude effect at sites C_z and P_z .

b) HEAD TILTED

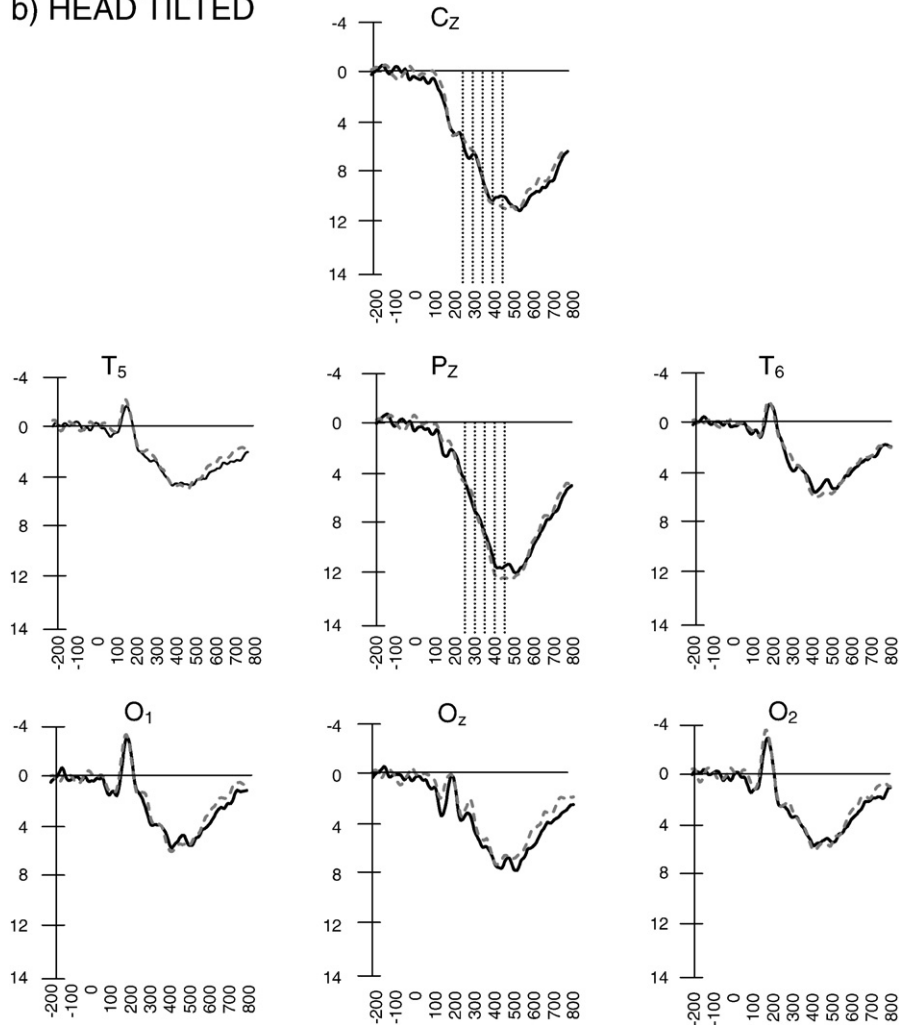


Fig. 5 (continued).

tilted condition of Experiment 2. However, ocular torsion is then also a natural contribution to the effects of head tilt previously demonstrated in behavioral literature, allowing for a consistent interpretation of our results in this context. Again, future research examining the contribution of torsional eye movements on the magnitude of the RFI may help to shed light on the integration of visual and vestibuloocular inputs for the perception of orientation.

To conclude, our findings provide electrophysiological support that global orientation context affects the perceived orientation of a stimulus during relatively late, post-perceptual stages of processing. In a general framework, a post-perceptual influence of global visual references in the external environment may render us less sensitive to the constantly fluctuating positions of our bodies, and allow us to maintain our relatively stable percept of an upright world. Pin-pointing when global orientation context effects are manifest allows us to better estimate when observers are vulnerable to such orientation context illusions, whether they are standing inside a tilted mystery cabin or navigating towards an approaching runway.

5. Experimental procedures

5.1. Experiment 1

5.1.1. Participants

Forty-one right-handed undergraduate students (22 women and 19 men, aged 18–28) at the University of British Columbia voluntarily participated in a two-hour session in exchange for \$20 (CAD). All participants had normal or corrected-to-normal vision, and none reported any neurological disorders. All procedures and protocols were in accordance with the University of British Columbia's Institutional Review Board.

5.1.2. Task

On each trial, observers were required to indicate whether the top of a rod, flashed briefly inside a square frame, was tilted CCW or CW from gravitational upright (Fig. 1). The experimenter informed participants that they should judge the tilt of the rod on each trial regardless of the orientation of the surrounding frame, make a prompt

decision even if they were unsure of the rod's tilt, and respond as accurately as possible.

5.1.3. Apparatus

Observers sat approximately 65 cm away from a Macintosh monitor that displayed stimuli generated by a Pentium PC using the VAPP stimulus presentation system (<http://nilab.psychiatry.ubc.ca/vapp/>). We took several steps to increase the likelihood that observers would rely on the frame in the RFI displays to perceive the direction of upright instead of using the upright context given by surfaces in the external laboratory or monitor. First, we mounted a black cardboard annulus with an inner radius of approximately 20° over the rectangular monitor to create a viewing window with inner and outer circular contours. In addition, to limit the availability of the upright context of the experimental room, we switched off the room lights several minutes before beginning each experimental session.

5.1.4. Design, stimuli, and procedure

Observers participated in seven blocks of sixty trials for a total of 420 trials each. All stimuli were black on a white background. Each trial began with a square frame subtending 10° visual angle displayed in the center of the circular viewing window. We presented the rod and frame in temporal succession to record the neural activity associated with the onset of the rod alone as a function of frame orientation. The frame was equally likely to be tilted 15° CCW or 15° CW from vertical on each trial.

Behavioral response time data collected during pilot studies showed that the context of the tilted frame had the largest effect on the perceived orientation of the rod when it was visible approximately 1200 ms before the 100 ms rod stimulus appeared. To avoid confounding neural activity associated with the perception of the rod stimulus with neural activity associated with expectancies from a learned temporal “rhythm” of repeated rod and frame durations, we jittered the length of the frame presentation before and after the 100 ms rod stimulus on each trial. 1000–1400 ms after the onset of the frame, a rod subtending 1.5° of visual angle appeared for 100 ms in the center of the frame.

All lines making up the RFI displays subtended .25° of visual angle in width. We chose to use a small rod and a relatively large surrounding frame so that there was a large spatial gap between the stimulus and context. This helped to minimize the likelihood that early local interactions could account for any observed differences in correct response times or cortical activity. The rod was tilted 8° CCW at random on half of the trials in each block, and 8° CW on the other half of trials. The frame remained on the screen for 800–1200 ms after the rod had offset.

On each trial, observers pressed the left button on a hand-held controller with the left thumb if the rod was tilted CCW, or the right button with the right thumb if the rod was tilted CW from gravity, and we allowed them up to 3000 ms after the offset of the frame to make their choice. We measured their response time and accuracy using a remote computer linked to the hand-held controller. The four possible combinations of frames (CCW or CW) and rods (CCW or CW) were presented at random with equal probability in each block. Participants first completed a block of sixty practice trials with at least 85% accuracy before they were permitted to begin the experimental trials.

5.1.5. Electrophysiological recording

Concurrently with behavioral measures of RT and accuracy, we recorded electroencephalograms (EEGs) from multiple scalp locations using 20 tin electrodes mounted in an elastic cap. All EEG activity was recorded with reference to the left mastoid, amplified using a Grass Instruments, Model 12 Neurodata Acquisition System with a band pass of .1–30 Hz (half-amplitude cut-offs), and digitized on-line at a sampling rate of 256 samples-per-second. To ensure proper eye fixation, vertical and horizontal electro-oculograms (EOGs) were also recorded; the vertical EOGs from two electrodes, one inferior to the left eye and one inferior to the right eye, and the horizontal EOGs from two electrodes on each of the left and right outer canthi. All electrode impedances were kept below 5 k Ω . Off-line, computerized artifact rejection was used to eliminate trials during which detectable eye movements (>1°), blinks, potentials, or amplifier blocking occurred. For each participant, EEGs were time-locked to a 3000 ms epoch centered around the presentation of the rod stimulus on each trial. Subsequently, all EEGs were algebraically re-referenced to the average of the left and the right mastoid signals, and filtered with a low-pass Gaussian filter (25.6 Hz half-amplitude cut-off) to eliminate high-frequency artifacts in the waveforms.

5.2. Experiment 2

Twenty-two right-handed undergraduate students (11 women and 11 men, aged 18–27) at the University of British Columbia voluntarily participated in a two-hour session in exchange for \$20 (CAD). All participants had normal or corrected-to-normal vision, and none reported any neurological disorders. All behavioral and ERP methods in Experiment 2 were identical to Experiment 1, except that each observer in Experiment 2 participated in two conditions, head upright and head tilted 15°, with five consecutive blocks of sixty trials for a total of 300 trials in each condition. Pilot data showed no evidence that the CCW or CW direction of head tilt had dissimilar effects on behavioral or electrophysiological measures, so we counterbalanced the order of conditions (head upright and head tilted) within participants, and the direction of head tilt (CCW and CW) between participants. At the start of each condition, they each completed one block of 60 practice trials with at least 85% accuracy. The experimenter continuously monitored the position of each participant's head with reference to a 15° line positioned on the wall behind the observer, adjusted to be in-line with the center of each individual's head. Observers were able to right their heads between head tilted blocks in order to help ensure their comfort.

REFERENCES

- Adams, D.L., Sincich, L.C., Horton, J.C., 2007. Complete pattern of ocular dominance columns in human primary visual cortex. *J. Neurosci.* 27 (39), 10391–10403.
- Allison, R.S., Howard, I.P., Zacher, J.E., 1999. Effect of field size, head motion, and rotational velocity on roll vection and illusory self-tilt in a tumbling room. *Perception* 28, 299–306.

- Asch, S.E., Witkin, H.A., 1948. Studies in space orientation: I. Perception of the upright with displaced visual fields. *J. Exp. Psychol.* 38, 325–337.
- Beh, H., Wenderoth, P., Purcell, A.T., 1971. The angular function of a rod-and-frame illusion. *Percept. Psychophys.* 9, 353–355.
- Bischof, N., 1974. Optic vestibular orientation to the vertical. In: Kornhuber, J.J. (Ed.), *Handbook of Sensory Physiology*, 6, Pt. 2. Springer-Verlag, New York, pp. 155–190.
- Bledowski, C., Prvulovic, D., Hoehstetter, K., Scherg, M., Wibral, M., Goebel, R., Linden, D.E.J., 2004. Localizing P300 generators in visual target and distractor processing: a combined event-related potential and functional magnetic resonance imaging. *J. Neurosci.* 24 (42), 9353–9360.
- Cheng, K., Waggoner, R.A., Tanaka, K., 2001. Human ocular dominance columns as revealed by high-field functional Magnetic Resonance Imaging. *Neuron* 32 (2), 359–374.
- Coles, M.G.H., Rugg, M.D., 1995. Event-related potentials: an introduction. In: Rugg, M.D., Coles, M.G.H. (Eds.), *Electrophysiology of Mind: Event-Related Potentials and Cognition*. In: New York, Oxford.
- Corbett, J.E., Enns, J.T., 2006. Observer pitch and roll influence the rod and frame illusion. *Psychon. Bull. Rev.* 13 (1), 160–165.
- Corbett, J.E., Handy, T.C., Enns, J.T., 2009. When do we know which way is up? The time course of orientation perception. *Vis. Res.* 49 (1), 28–37.
- Daini, R., Wenderoth, P., 2008. Orientation illusions vary in size and direction as a function of task-dependent attention. *Percept. Psychophys.* 70 (7), 1289–1297.
- DiLorenzo, J.R., Rock, I., 1982. The rod-and-frame effect as a function of the righting of the frame. *J. Exp. Psychol. Hum. Percept. Perform.* 8 (4), 536–546.
- Donchin, E., Coles, M.G.H., 1988. Is the P300 component a manifestation of context updating? *Behav. Brain Sci.* 11, 355–372.
- Dyde, R.T., Milner, D.A., 2002. Two illusions of perceived orientation: one fools all of the people some of the time; the other fools all of the people all of the time. *Exp. Brain Res.* 144 (4), 518–527.
- Ebenholtz, S.M., 1977. Determinants of the rod and frame effect: the role of retinal size. *Percept. Psychophys.* 22 (6), 531–538.
- Ebenholtz, S.M., Callan, J.W., 1980. Modulation of the rod and frame effect: retinal angle vs. apparent size. *Psychol. Res.* 42 (4), 327–334.
- Guerraz, M., Poquin, D., Ohlmann, T., 1998. The role of head-centric spatial reference with a static and kinetic visual disturbance. *Percept. Psychophys.* 60 (2), 287–295.
- Guerraz, M., Yardley, L., Bertholon, P., Pollak, L., Rudge, P., Gresty, M.A., Bronstein, A.M., 2001. Visual vertigo: symptom assessment, spatial orientation and postural control. *Brain* 124 (8), 1646–1656.
- Hafstrom, A.C.A., Fransson, P.A., Karlberg, M., Magnusson, M., 2004. Ipsilesional visual field dependency for patients with vestibular schwannoma. *NeuroReport* 15 (14), 2201–2204.
- Handy, T.C., 2005. *Event-Related Potentials: a Methods Handbook*. MIT Press, Cambridge.
- Handy, T.C., Mangun, G.R., 2000. Attention and spatial selection: electrophysiological evidence for modulation by perceptual load. *Percept. Psychophys.* 62 (1), 175–186.
- Haynes, J.D., Rees, G., 2005. Predicting the orientation of invisible stimuli from activity in human primary visual cortex. *Nat. Neurosci.* 8 (5), 686–691.
- Heinrich, S.P., Aertsen, A., Bach, M., 2008. Oblique effects beyond low-level visual processing. *Vis. Res.* 48, 809–818.
- Heinze, H.J., Mangun, G.R., Burchert, W., Hinrichs, H., Scholz, M., Münte, T.F., Gös, A., Johannes, S., Scherg, M., Hundeshagen, H., Gazzaniga, M.S., Hillyard, S.A., 1994. Combined spatial and temporal imaging of spatial selective attention in humans. *Nature* 392, 543–546.
- Hubel, D.H., Wiesel, D.N., 1962. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* 160 (1), 106–154.
- Johnson Jr., R., 1986. A triarchic model of P300 amplitude. *Psychophysiology* 23, 367–384.
- Kennedy, P.M., Carlsen, A.N., Inglis, J.T., Chow, R., Franks, I.M., Chua, R., 2003. Relative contributions of visual and vestibular information on the trajectory of human gait. *Exp. Brain Res.* 153, 113–117.
- Li, W., Matin, L., 2005. Two wrongs make a right: linear increase of accuracy of visually-guided manual pointing, reaching, and height-matching with increase in hand-to-body distance. *Vis. Res.* 45, 533–550.
- Lopez, C., Lacour, M., Magnan, J., Borel, L., 2006. Visual field dependence–independence before and after unilateral vestibular loss. *NeuroReport* 17 (8), 797–803.
- Luck, S.J., Hillyard, S.A., 1995. The role of attention in feature detection and conjunction discrimination: an electrophysiological analysis. *Int. J. Neurosci.* 80 (1–4), 281–297.
- Mangun, G.R., Hillyard, S.A., 1991. Modulation of sensory-evoked brain potentials provide evidence for changes in perceptual processing during visual spatial priming. *J. Exp. Psychol. Hum. Percept. Perform.* 17, 1057–1074.
- Merker, B.H., Held, R., 1981. Eye torsion and the apparent horizon under head tilt and visual field rotation. *Vis. Res.* 21, 543–547.
- Milner, A.D., Goodale, M.A., 1995. *The Visual Brain in Action*. Oxford University Press, London.
- Roeber, U., Widmann, A., Trujillo-Barreto, N.J., Herrmann, C.S., O'Shea, R.P., Schöger, E., 2008. Early correlated of visual awareness in the human brain: time and place from event-related brain potentials. *J. Vis.* 8(3) (21), 1–12.
- Smith, A.T., Jeffreys, D.A., 1978. Size and orientation specificity of transient visual evoked potentials in man. *Vis. Res.* 18, 651–655.
- Soltani, M., Knight, R.T., 2000. Neural origins of the P300. *Crit. Rev. Neurobiol.* 14, 199–224.
- Spinelli, D., Antonucci, G., Daini, R., Fanzon, D., Zoccolotti, P., 1995. Modulation of the rod-and-frame illusion by additional external stimuli. *Perception* 24 (10), 1105–1118.
- Vibert, D., Häusler, R., Safran, A.B., 1999. Subjective visual vertical in peripheral unilateral vestibular diseases. *Journal of Vestibular Research* 9 (2), 145–152.
- Vogel, E.K., Luck, S.J., Shapiro, K.L., 1998. Electrophysiological evidence for a postperceptual locus of suppression during the Attentional Blink. *J. Exp. Psychol. Hum. Percept. Perform.* 24 (6), 1656–1674.
- Walter, E., Dassonville, P., 2008. Visuospatial contextual processing in the parietal cortex: an fMRI investigation of the induced Roelofs effect. *NeuroImage* 42 (4), 1686–1697.
- Wenderoth, P., Beh, H., 1977. Component analysis of orientation illusions. *Perception* 6, 57–75.
- Wenderoth, P., Johnstone, S., 1987. Possible neural substrates for orientation analysis and perception. *Perception* 16, 693–709.
- Wenderoth, P., Smith, S., 1999. Neural substrates of the tilt illusion. *Aust. N. Z. J. Ophthalmol.* 27, 271–274.
- Witkin, H.A., 1949. Perception of body position and the position of the visual field. *Psychol. Monogr.* 63, 1–63.
- Woldorff, M., Fox, P., Matzke, M., Lancaster, J., Veeraswamy, J., Zamarripa, F., Seabolt, M., Glass, T., Gao, J., Martin, C., Jerabek, P., 1997. Retinotopic organization of the early visual spatial attention effects as revealed by PET and ERPs. *Hum. Brain Mapp.* 5, 280–286.
- Yardley, L., 1990. Contribution of somatosensory information to perception of the visual vertical with body tilt and rotating visual field. *Percept. Psychophys.* 48, 131–134.
- Young, L.R., Oman, C.M., Dichgans, J.M., 1975. Influence of head orientation on visually induced pitch and roll sensation. *Aviat. Space Environ. Med.* 46, 264–269.