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RESEARCH ARTICLE

Differential effects of vestibular processing on orienting exogenous and endogenous covert visual attention

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Abstract

Recent research highlights the overwhelming role of vestibular information for higher order cognition. Central to body perception, vestibular cues provide information about self-location in space, self-motion versus object motion, and modulate the perception of space. Surprisingly, however, little research has dealt with how vestibular information combines with other senses to orient one's attention in space. Here we used passive whole body rotations as exogenous (Experiment 1) or endogenous (Experiment 2) attentional cues and studied their effects on orienting visual attention in a classical Posner paradigm. We show that—when employed as an exogenous stimulus—rotation impacts attention orienting only immediately after vestibular stimulation onset. However, when acting as an endogenous stimulus, vestibular stimulation provides a robust benefit to target detection throughout the rotation profile. Our data also demonstrate that vestibular stimulation boosts attentional processing more generally, independent of rotation direction, associated with a general improvement in performance. These data provide evidence for distinct effects of vestibular processing on endogenous and exogenous attention as well as alertness that differ with respect to the temporal dynamics of the motion profile. These data reveal that attentional spatial processing and spatial body perception as manipulated through vestibular stimulation share important brain mechanisms.

Keywords Vestibular · Cognition · Exogenous attention · Endogenous attention

Introduction

A fundamental role of attention is the ability to direct one's focus towards relevant stimuli in the environment, thus facilitating perception and action orienting. Importantly, to orient attention in space, information about the position and direction of the eyes and the head, which is provided by the vestibular system and its afferents, needs to be effectively combined with incoming signals from other senses (i.e. visual and auditory cues) to inform processes related to spatial perception and attention and, eventually, motor responses. Despite this obvious vestibular contribution to attention and the growing body of research on vestibular cognition, vestibular effects on attentional processing have received only sparse consideration.

Early insight into the relationship between vestibular function and attention has initially been provided by clinical research with patients suffering from hemispatial neglect, i.e. a deficit in attending to the contralesional side of space usually following right brain damage (Halligan et al. 1989). In these patients, it has been shown that attentional deficits decrease partially after caloric vestibular stimulation (Bottini et al. 2001; Cappa et al. 1987; Karnath and Dieterich 2006; Vallar et al. 1990). In healthy volunteers, several findings support the presence of vestibular effects on attention (Ferrè et al. 2013; Hartmann et al. 2012b; Lewald and Karnath 2001). Using different paradigms (temporal order judgement (TOJ), line bisection, mental number line, sound localisation) and different forms of vestibular stimulation [caloric vestibular stimulation (CVS), galvanic vestibular stimulation

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(GVS), stimulations that interact with vestibular processing: muscle vibration, large-field visual stimulation (background optic flow), or physiological vestibular stimulation via a rotating chair (motion platform)], these studies converge in showing that vestibular stimulation biases spatial processing and, in particular, attention orienting to one side of space, in accordance with the stimulation method used[1]. Thus, GVS directs attention in the direction of the anode (Ferrè et al. 2013), cold CVS—to the contralateral side (Lewald and Karnath 2000), and passive translations and rotations in the direction of self-motion (Hartmann et al. 2012b; Lewald and Karnath 2001) [with a few exceptions where no such effects were observed (Rorden et al. 2001), or the effect was inconsistent (Shuren et al. 1998)].

In the present study, we address some important points, omitted in previous research. Using a human motion platform, we investigate whether vestibular stimulation provided via passive whole body rotations (i.e. Prsa et al. 2012; Gale et al. 2016; Kaliuzhna et al. 2016) impacts orienting of attention in a classical cue-to-target Posner task (Posner 1980), and whether it can act effectively an as exogenous (Experiment 1) and/or an endogenous (Experiment 2) cue. Crucially, we explore how vestibular inputs modulate attention over time. This is relevant because vestibular stimulation is dynamic and provided over extended stimulation periods (due to the way in which vestibular organs signal self-motion) (Goldberg and Fernández 2000) as opposed to more well-known effects based on other modalities (i.e. visual, auditory or tactile cues) that are most often not modulated over time and have been presented in attention studies for very short durations (some studies only for a few milliseconds). It is not known whether vestibular effects on attention orienting occur throughout the period of the vestibular stimulus and are of similar strength or whether they are only present during specific moments of rotation (for example at the moment of the strongest discharge of vestibular organs (Goldberg and Fernández 2000) or at the moment of the discharge onset).

Materials and methods

Participants

Fifteen healthy, right-handed (Oldfield 1971) adults naïve to the purpose of the study, with normal or corrected vision and no history of inner ear disease, participated in Experiment 1 (3 females, mean age 27.4 ± 3.6 years), and 14 others in Experiment 2 (4 females; mean age 25 ± 2.8 years). All participants gave informed consent and received monetary retribution at 20 CHF/h. The studies were approved by a local ethics committee and were conducted in accordance with the Declaration of Helsinki.

Experimental setup

The same experimental setup was used for both experiments. The experiments took place in a sound-shielded room in complete darkness. Participants were comfortably restrained by a 5-point racing harness in the chair of a servo-controlled (PCI-7352) rotation platform (±0.1° precise positioning) (Prsa et al. 2012; van Elk and Blanke 2013). Participants' heads were aligned with their bodies' z axis and positioned at the centre of rotation. Head movements were prevented using a forehead bar and a chin rest. A 22″ computer display was mounted 40 cm in front of the participants. Stimuli were presented on the screen via an on-board computer using custom Python-based software (ExpyVR, http://lnco.epfl.ch/expyvr). Participants used a keyboard to respond. White noise was played to participants through headphones during the experiment to prevent auditory cues.

Experimental procedure

In both experiments, participants performed a Posner task, in which they were asked to respond as fast and as correctly as possible to a grey circle appearing either on the right or on the left side of the screen (see below for details). Participants pressed the left arrow button on the keyboard with the index finger if the target appeared on the left, and the right arrow button with the middle finger if the target appeared on the right. A central fixation cross was present at all times to minimise eye movements and participants were requested to maintain fixation on it throughout the trial.

Experiment 1

In Experiment 1 we investigated whether CW or CCW rotations would act as an exogenous attentional cue, affecting the accuracy and the speed of participants' target detection. Performance in stationary trials without any chair rotation was used as a baseline condition (i.e. neutral condition of the classical Posner task). Participants were instructed to respond as fast and as correctly as possible indicating the side where the target appeared. This was done by pressing either the right or the left arrow keys of a keyboard with

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[1] It is possible that other cognitive processes in addition to (or instead of) attention account for the results in some of these tasks. Such processes could involve the spatial-numerical association of response codes (SNARC effect) (Hartmann et al. 2012a) and the effect of stimulation on spatial reference frames (Ferrè et al. 2013; Fink et al. 2003).

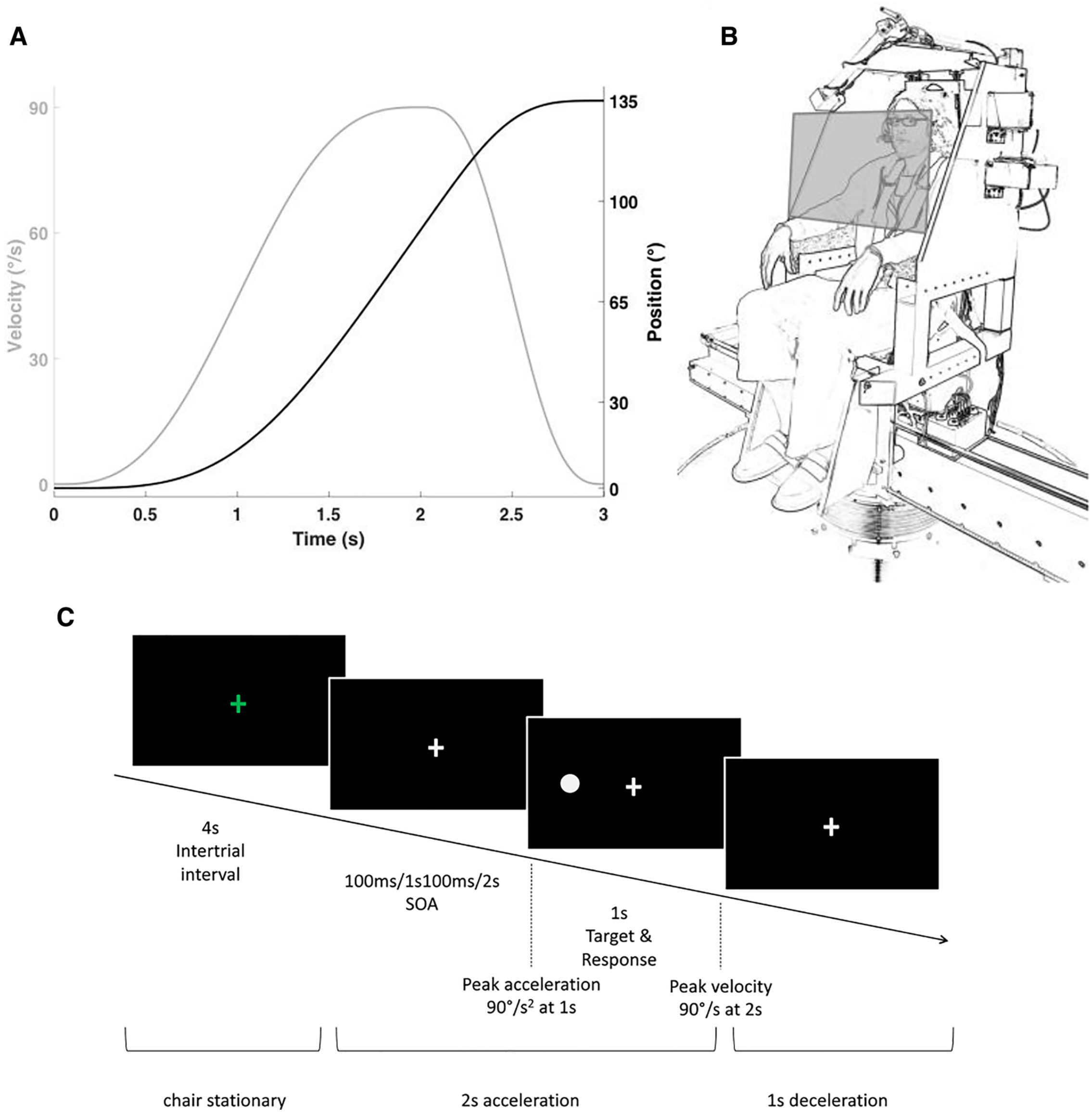

Fig. 1 Schematic representation of an experimental trial and the setup for both experiments. **a** Position and velocity profiles of the rotation stimulus. **b** View of participant in the rotating chair with a monitor in front. **c** Experimental trial. A green fixation cross indicated the beginning of a trial. Participants had to respond as fast as possible whether a grey dot appeared on the right or on the left part of the screen

the index or middle finger of their right hand (i.e. the left arrow was always pressed with the index finger, and the right arrow—with the middle finger). Participants were told that on some trials the chair would move and on others it would remain stationary. They were asked to ignore the chair movements.

The sequence of an experimental trial is represented in Fig. 1. A green cross was presented in the centre of the screen. The trial started when the cross turned grey. On rotation trials, the rotation began at the same time as the cross changed colour. The rotating platform accelerated during 2 s and decelerated during 1 s. Peak acceleration ($90°/s^2$) occurred 1 s after the beginning of rotation [as previously used by us i.e. (Prsa et al. 2012; van Elk and Blanke 2012)] and peak velocity (90°/s) was reached at 2 s. The duration of each trial was 3 s. Participants were rotated 135°. The target was a grey circle (1.5 cm diameter) that appeared at 17° of visual angle either to the left or to the right of the fixation cross. To study the temporal relationship between vestibular cue and response modulation, on different trials the target appeared at either 100, 1100 or 2000 ms after the beginning of the trial. These periods were chosen to test potential vestibular effects immediately after rotation onset (i.e. 100 ms after the beginning of rotation), around peak acceleration (i.e. at 1000 ms), and during maximal velocity (i.e. at 2000 ms). In this way, we tested whether any vestibular effects on attentional processing were more strongly associated with the initial discharge of the vestibular organs, to their maximum discharge, or to the general duration of stimulation. The target was presented for 1 s during which the subject responded. When the trial ended, the cross turned green again. The inter-trial interval was of 4 s. During the task, participants were requested to keep fixation at the central cross and to try and suppress reflexive eye movements to the target.

There were nine experimental conditions: three cue-to-target delays (100, 1100, 2000 ms) by three rotation conditions (congruent rotation, incongruent rotation, stationary baseline). The chair rotation conditions were coded with respect to the side of target onset as: congruent (e.g. CCW/CW rotation + target appearing on the left/right part of the screen), incongruent (e.g. CCW/CW rotation + target appearing on the right/left part of the screen) and baseline (no-rotation + right/left side target) conditions. There was the same number of CCW and CW rotations and left and right side targets. Participants performed a total of 576 trials (64 trials per condition, i.e. the number of congruent, incongruent and baseline trials was the same) that were presented in a random order in four blocks (144 trials per block). The whole experiment lasted for about 90 min.

Experiment 2

The setup of Experiment 2 was the same as in Experiment 1, except that, crucially, in this experiment the rotation was used to orient attention endogenously. Thus, the participants were explicitly instructed that the direction of rotation (when present) would predict, on most of the trials, the side of target onset (i.e. Posner 1980) and were asked to covertly (i.e. without moving their eyes or head) shift their attention in the same direction as the rotation, while maintaining fixation of the central cross. Again, they had to respond as fast and as correctly as possible indicating the side on which the target appeared, by button press, as described for Experiment 1.

As in Experiment 1, there were three cue-to-target delays (100, 1000 and 2000 ms) occurring in three conditions: congruent, incongruent and baseline. Participants performed a total of 576 trials. Following the classical Posner paradigm, the distribution of trials was set so that the rotation predicted the side of target onset in 80% of the cases, thus yielding the following trials combinations: 312 congruent trials, 72 incongruent trials and 192 baseline (no-rotation) trials.

Statistical analysis

Normal distribution of the data in both experiments was confirmed by non-significant Shapiro–Wilk tests (all $p > 0.05$). For both experiments, we performed a two-way ANOVA, with cue-to-target delay as first factor (100, 1000, 2000 ms) and rotation type (congruent, incongruent, no-rotation) as second factor on the accuracy and the reaction times values. For Experiment 1, Mauchly's test of sphericity indicated that the variance homogeneity assumption was violated for the main effects (both $p = 0.002$), but not the interaction ($p = 0.57$); the results are thus reported with the Greenhouse–Geisser correction. Newman–Keuls analyses were used for post-hoc tests.

Results

Experiment 1: exogenous attention

Reaction times

The ANOVA run on reaction times (RT) revealed a significant main effect of cue-to-target delay ($F(2, 28) = 56.205$, $p < 0.0001$, partial $\eta^2 = 0.8$), of rotation type ($F(2, 28) = 69.944$, $p < 0.0001$, partial $\eta^2 = 0.83$) and a significant interaction ($F(4, 56) = 9.9871$, $p < 0.0001$; partial $\eta^2 = 0.42$). Post-hoc comparisons performed on the main effects showed that participants were significantly faster when the visual target appeared at 1100 ms and 2000 ms compared to 100 ms (both $p < 0.001$), with no difference between the former two conditions ($p = 0.08$). Participants were also faster in the two rotation conditions (no difference between congruent and incongruent, $p = 0.9$) with respect to the no-rotation baseline condition ($p < 0.001$ for both comparisons).

Post-hoc analysis performed on the significant cue-to-target delay × rotation type interaction revealed the following results (see Fig. 2). First, there was no difference between the congruent and the incongruent conditions for any cue-to-target delays (100 ms: $p = 0.14$; 1100 ms: $p = 0.72$; 2000 ms: $p = 0.45$). Next, examining how participants' reaction times changed in the three rotation conditions as a function of cue-to-target delay, we found that for both the congruent and the incongruent conditions, participants were significantly faster the later the target appeared (i.e. faster at 1100 ms than at 100 ms, and even faster at 2000 ms) (all $p < 0.001$). However, in the no-rotation baseline condition participants responded equally fast at the two late cue-to-target delays ($p = 0.93$), and at both these delays they were faster with respect to 100 ms (both $p < 0.001$).

To refine the analysis and to directly compare the effect of congruent vs. incongruent rotations, we conducted further ANOVA including only the reaction times for the congruent and the incongruent conditions. There was a significant main effect of cue-to-target delay as reported earlier ($F(2, 28) = 47.801$, $p < 0.0001$, partial $\eta^2 = 0.77$); and, more importantly, a significant time × rotation interaction ($F(2, 28) = 3.5109$, $p = 0.044$, partial $\eta^2 = 0.2$). Post-hoc analysis

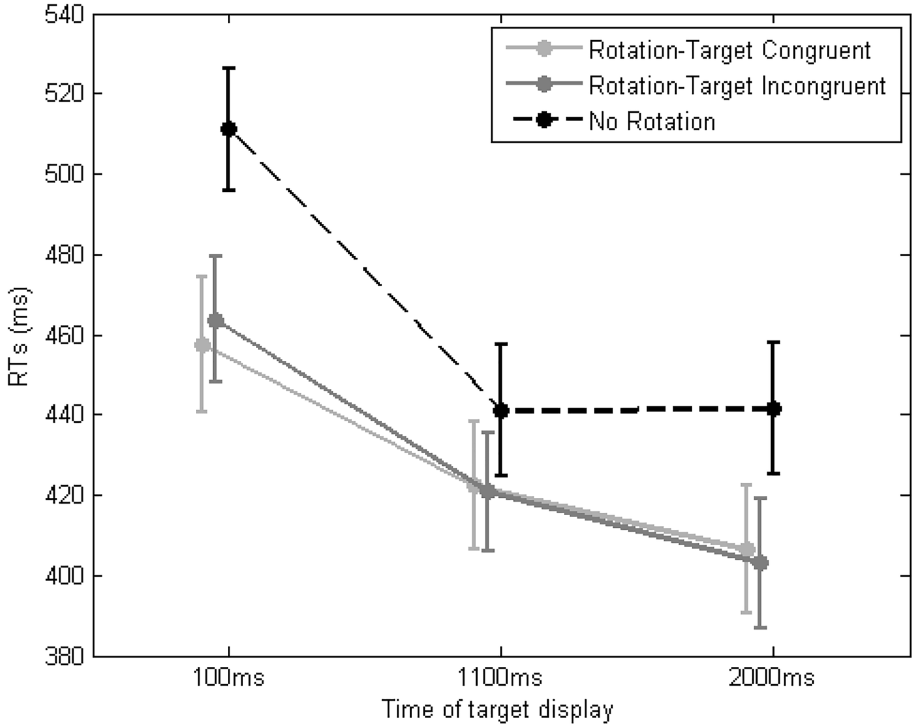

Fig. 2 Experiment 1. Mean reaction times and standard errors (shown by error bars) for the congruent, incongruent and the no-rotation condition at the three cue-to-target delays

showed that participants were significantly faster in the congruent condition than in the incongruent condition, but only at 100 ms ($p = 0.028$) (at 1100 ms: $p = 0.58$; at 2000 ms: $p = 0.24$).

Finally, we controlled for several biases in the present data. To check for any effects of the finger used to respond (middle or index) we ran a three-way ANOVA (three levels of cue-to-target delay by three levels of rotation types by two levels of finger used). No main effect of finger ($F(1, 14) = 3.3665$, $p = 0.09$), or interaction of the finger used with other factors was found to be significant. To control for any effect of the direction of rotation we ran an ANOVA comparing RTs for CW, CCW, and no-rotation conditions ($F(2, 28) = 66.093$, $p < 0.0001$). Post-hoc comparisons showed no difference between CW and CCW rotations ($p = 0.89$); RTs during CW and CCW rotations were significantly faster than during the no-rotation baseline, in accordance with the above analysis (both $p < 0.0001$).

Accuracy

Overall, the participants made very few errors (1.2%). The two-way ANOVA showed a significant main effect of the cue-to-target delay ($F(2, 28) = 4.0837$, $p = 0.028$, partial $\eta^2 = 0.22$), participants being equally accurate at 1100 ms and 2000 ms (post-hoc Newman–Keuls comparison, $p = 0.58$), and significantly less accurate in the 100 ms cue-to-target delay condition ($p = 0.04$ and $p = 0.02$, respectively). The ANOVA also yielded a significant main effect of rotation ($F(2, 28) = 11.718$, $p < 0.001$, partial $\eta^2 = 0.46$) with participants being equally accurate in the congruent and the incongruent conditions ($p = 0.24$), and significantly more accurate in the two rotation conditions as compared to the no-rotation baseline condition (both $p < 0.01$). No interaction was found ($p = 0.69$).

Experiment 2: endogenous attention

Reaction times

Due to the design of the endogenous attention task which necessitates an imbalance in the number of valid and invalid trials we used the linear mixed effects model approach to analyse the results (Kliegl et al. 2011). We used R software (version 3.5.1) and the *lmer* program of the *lme4* package (Bates and Maechler 2010) to perform the analysis. Following Barr et al. (2013) we started with the maximal random effect structure and applied the first model that converged (Barr et al. 2013); thus reaction times were modelled as a function of rotation type, cue-to-target delay and their interaction, with correlated intercepts and slopes for the two fixed factors as random effects. An ANOVA on the model revealed the main effects and the interaction to be significant: rotation type $F(2, 12.9) = 55.6$, $p < 0.0001$; cue-to-target delay $F(2, 15.1) = 30.8$, $p < 0.0001$; interaction $F(4, 7282.8) = 31.9$, $p < 0.0001$ (Fig. 3). The fixed effect contrasts further showed that the later the target appeared, the faster participants responded (100–1000 ms $p = 0.0001$ and 1000–2000 ms

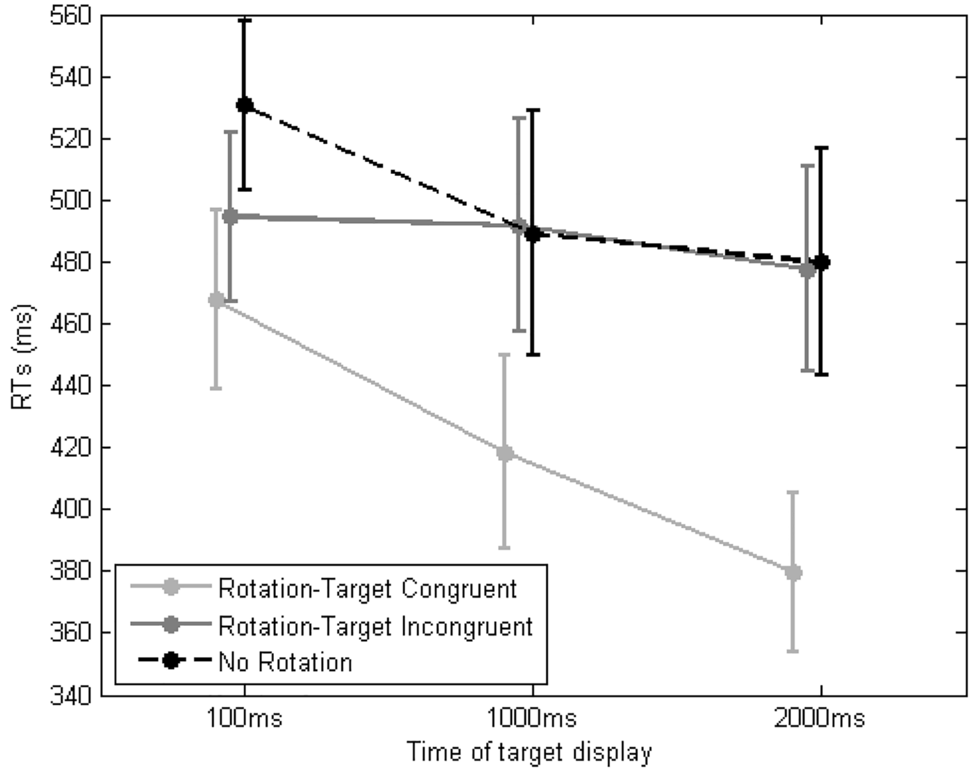

Fig. 3 Experiment 2. Mean reaction times and standard error (shown by error bars) for the congruent, incongruent, and the no-rotation condition at the three cue-to-target delays

$p = 0.0001$), and that participants were significantly faster in the congruent condition as compared to the incongruent and baseline conditions (both $p < 0.0001$), with no difference between the latter two ($p = 0.63$).

An examination of the rotation type × cue-to-target delay interaction showed that at all delays participants were significantly faster in the congruent condition as compared to the other two (all $p < 0.005$). Further, there was a significant difference between the incongruent and the baseline condition but only at 100 ms ($p = 0.005$). Finally, we examined how participants' reaction times changed in each of the three rotation conditions as a function of cue-to-target delay. In the congruent condition, RTs became shorter at increasing cue-to-target delays (all p values < 0.0001). This effect was absent in the incongruent condition, where RTs did not differ depending on the cue-to-target delay (all $p > 0.12$). In the no-rotation baseline condition, in keeping with results from Experiment 1, participants were significantly faster when the target appeared at 1000 ms and 2000 ms compared to 100 ms (both $p < 0.0001$), with no difference between the former two ($p = 0.32$).

Accuracy

Overall participants made few errors (2.6%). Fitting a generalised linear mixed effects model to accuracy data using the same structure as above revealed no significant differences between experimental conditions.

Discussion

In two experiments, we examined how the application of a bodily cue—vestibular stimulation in the form of passive whole body yaw rotations—modulates specific attentional processes. We report three main findings. First, vestibular stimulation leads to behavioural facilitation associated with faster responses in Experiment 1 and 2 and higher accuracy in Experiment 1, as compared to a baseline condition without any rotation. This general and alerting vestibular effect resulted in faster target detection, independently of whether the rotation direction was congruent or incongruent with the side of target onset. Second, we demonstrate that passive whole body yaw rotations may act as an exogenous cue, as evidenced by orienting attention in the direction of rotation. This effect was characterized by faster target detection, but was only found for cues presented immediately after vestibular stimulation onset (shortest cue-to-target delay). Our data revealed a third distinct vestibular effect on attention that was present for all tested delays, compatible with a robust impact on endogenous attentional processes (however, see below for an alternative interpretation).

Vestibular stimulation leads to general arousal

The present data show that both congruent and incongruent conditions in Experiment 1 yielded faster responses and fewer errors than the no-rotation baseline condition. We interpret this vestibular effect as an increase in arousal/vigilance provoked by vestibular stimulation, resulting in increased alertness and general attention to the task. Previous research shows that arousal (produced by e.g. emotional stimuli, loud sounds or physical exercise) decreases reaction times to target stimuli (Brown et al. 2014; Garg et al. 2013; Max et al. 2015). Vestibular stimulation, in the form of passive whole body rotation (or tilt), has previously been reported to produce arousal effects [as measured by heart-rate changes and skin conductance response (Carmona et al. 2008; Sloan et al. 2001)]. We believe vestibular stimulation may lead to general arousal as part of a network dedicated to providing optimal reactivity in situation where rapid movement is required (e.g. threat avoidance, attack) or where movement might lead to damage (e.g. fainting, falling).

Exogenous attention orienting and vestibular stimulation

Attention allows us to detect events in specific spatial locations, thus enhancing the speed and quality of their processing and preparing humans for relevant actions. When turning one's head or being turned in a particular direction, previous research suggests that attention is automatically oriented in that direction. Thus, Karnath et al. (1996) showed that ocular exploration was biased to one side of space by both CVS and neck muscle stimulation and Ferrè et al. (2013) found GVS to influence the perceived central point of a line (in a line bisection task). In addition, background motion of optic flow directs attention to the incoming field (i.e. in the putative direction of induced self-motion) (Watanabe 2001). Extending this line of work, we found a spatial orienting effect associated with vestibular stimulation in Experiment 1 at the shortest cue-to-target delay (100 ms), participants being significantly faster in the congruent than in the incongruent condition. Vestibular stimulation can thus act as an endogenous crossmodal cue for visual attention, similarly to other modalities (Santangelo et al. 2006, 2008; Spence 2010).

The present data also show that for exogenous vestibular attention the onset of rotation is critical, whereas peak acceleration of vestibular stimulation has no particular effect on attention orienting. Thus, we found no visuo-vestibular attention orienting effects for longer cue-to-target delays, at 1100 ms and 2000 ms after rotation onset. Although not directly comparable, we note that previous research showed that exogenous cueing effects are maximal between 50 and 200 ms and may continue after 300 ms (Spence 2010). Former studies on cross-modal attention orienting have also shown that the magnitude of the orienting effect depends on the spatial correspondence between the cue and the target stimulus (Prime et al. 2008; Spence 2010). For example, if an auditory cue comes from a more eccentric location than that in which the visual target will appear (although both appear on the same side of space), the facilitation effect is dampened (Gray et al. 2009). Both effects (as well as inhibition of return) (Klein 2000) may also play a role in the present vestibular investigation. Finally, a vestibular cue is first of all an endogenous cue, and as such rotation does not seem to guide attention to a precise location in space, but rather a direction. This diffuse attentional spotlight may further dissipate as the rotation profile progresses.

Endogenous attention orienting

When vestibular information was explicitly made task-relevant participants were significantly faster in the congruent as compared to the incongruent and baseline conditions and this for all tested cue-to-target delays. Our results differ somewhat from classical findings on endogenous attention orienting, because we find no RT or accuracy costs when participants are attending to the uncued location. That is, in our study participants are not slower in the incongruent condition as compared to the no-rotation baseline condition, and sometimes even faster in the former than in the latter (at 100 ms). The observed general facilitation induced by vestibular inputs may be relevant, as increased general arousal during rotation may compensate for a misinformative cue, thus reducing the cost in the incongruent condition.

Concerning the timing of endogenous attention orienting, Green and Woldorff (2012) showed that early (≤ 100 ms) orienting effects of an arrow cue are driven by slowing of RTs in the incongruent condition, whereas facilitatory effects from congruent cues emerge only at later (≥ 300 ms) stages (tested under stationary conditions without any motion of the subjects). Our results show that whole-body rotation provides an orienting benefit even at early stages (100 ms), and that this effect is present independently of the incongruent condition.

In other words, the effect is not driven by slowing down of RTs in the incongruent condition, but by faster RTs in the congruent condition as compared to the baseline condition (with RTs in the incongruent condition remaining constant across stimulus presentation times). Interestingly, when the target appeared 100 ms after rotation onset, subjects reported (during post-experimental debriefing) that it either preceded the rotation or occurred at the same time as the rotation started. These observations emphasise the fact that despite being consciously perceived as uninformative, rotations maintained an orienting effect (i.e. successfully facilitated target detection). We suggest that this early facilitation effect is due to the fact that at 100 ms passive whole-body rotations may exert an exogenous effect on attention orienting, as we show in Experiment 1. The observed difference between the congruent and incongruent conditions is thus a combined exogenous-endogenous orienting effect (Berger et al. 2005).

Stimulus–response compatibility effects

Some of our results may be explained by a confound in the correspondence between the response dimension (index–middle finger, i.e. left–right response), the direction of rotation (CW-CCW, i.e. left–right side of space) and the side of stimulus onset (left–right) (i.e. response priming, or the Simon effect) (Proctor and Reeve 1990). Thus, faster reaction times in the congruent condition may be due to the direction of rotation (e.g. CCW → left) priming the response associated with that side of space (left → index finger), resulting in a response speed advantage when the target appears e.g. on the left. Slower responses in the incongruent condition would result from a conflict between the primed side of response (e.g. left) and the side of target onset (right). Unfortunately, our design of Experiment 2 does not allow to discriminate between endogenous orienting and motor priming. A design based on stimulus discrimination or an orthogonal experimental design, where the dimension of the target (e.g. target appearing to the left or right either above or below the screen midline) would not overlap with the dimension of the response (e.g. index finger for above targets, middle finger for below targets) would remedy this confound.

Stimulus–response compatibility seems unlikely in our exogenous Experiment 1. On the one hand, the effect we observe at 100 ms is not only smaller in magnitude than cross-modal attentional effects, but also smaller than the usual Simon effects (approx. 25 ms) (De Jong et al. 1994). If both attention orienting and the Simon effect are indeed present, we would expect a larger, not a smaller, effect, as the two would be additive. On the other hand, the absence of an effect at later cue-to-target delays also speaks against both response priming or attention orienting.[2]

Anticipation effect

In both Experiments 1 and 2 we also observe an anticipation effect: the later the stimulus appears the faster participants respond. This effect has also been observed by earlier authors (Green and Woldorff 2012; Posner 1980; Posner et al. 1980), with RTs decreasing in both congruent (decreasing RTs until about 300 ms of cue-target delay) and incongruent conditions (decreasing RTs until about 500 ms of cue-target delay), although on a different time-scale compared to the present data. We propose that this effect in the present experiments is due to participants anticipating the target onset when it is not displayed at 100 ms. Interestingly, during rotation this effect is present for both longer cue-to-target delays: participants are faster at 1100/1000 ms than at 100 ms and are even faster at 2000 ms (in Experiment 2 the effect is only present for the congruent condition). In the stationary baseline condition this effect is only present between the first and second presentation times, there being no additional benefit at 2000 ms, likely due to the additional temporal information contained in the vestibular stimulus (e.g. Fiebelkorn et al. 2011; Poulton 1950).

Slower RTs at the 100 ms cue-to-target delay could also be due to the attentional blink phenomenon (Raymond et al. 1992), which causes suppression in subsequent target detection 200–500 ms after an initial target has been presented. The change in the colour of the fixation cross could act as such an initial target in our paradigm. However, 100 ms targets fall outside the attentional blink window, and so should not be affected by attentional suppression.

Conclusion

In conclusion, our experiments show that a highly dynamical body stimulus—vestibular stimulation—in the form of passive whole body rotations, robustly impacts cognitive processing, here, attention orienting and/or motor priming. In order to precisely characterise vestibular effects on attention, future experiments will need to vary target presentation delays, stimulation profiles and target eccentricity, etc. to establish the conditions for the presence/absence of vestibular orienting. In addition, a more informative baseline condition could be used (instead of a static condition), which would lead to the same level of general arousal, but

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[2] It should be noted that the Simon effect can be rather transient and disappear after stimulus–response delays exceeding 350 ms (Jong et al. 1994). In our paradigm, however, vestibular stimulation is still present at every cue-to-target delay, so a Simon effect could still occur.

be direction unspecific (e.g. vibrations, up-down or forward–backward motion).

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