

Attention modulates event-related spectral power in multisensory self-motion perception

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ABSTRACT

Humans integrate visual and physical (vestibular and proprioceptive) cues to motion during self-motion perception. Theta and alpha-band oscillations have been associated with the processing of visual motion (e.g. optic flow). Alpha and beta-band oscillations have been shown to be associated with sensory-motor processing (e.g. walking). The present study examined modulation of theta, alpha, and beta oscillations while participants made heading direction judgments during a passive self-motion task which required selective attention to one of the simultaneously presented visual or physical motion stimuli. Attention to physical (while ignoring visual) motion produced a different time course of changes in spectral power compared to attention to visual (while ignoring physical) motion. We observed weaker theta event-related synchronization (ERS), as well as stronger beta and later onset of alpha event-related desynchronization (ERD) in the attend-physical condition compared to the attend-visual condition. We observed individual differences in terms of ability to perform the task. Specifically, some participants were not able to ignore or discount the visual input when visual and physical heading direction was incongruent; this was reflected by similar event-related spectral power for both conditions. The results demonstrated a possible electrophysiological signature of the time course of 1) cue conflict (congruency effects), 2) attention to specific motion cues, and 3) individual differences in perceptual weighting of motion stimuli (high-vs. low-accuracy effects).

1. Introduction

The perception of self-motion draws on the integration of the visual, vestibular and proprioceptive systems. These sensory inputs contribute through a continuous re-weighting process, which has been demonstrated in multisensory studies of self-motion perception (Angelaki et al., 2009; Butler et al., 2010; De Winkel et al., 2017; Morgan et al., 2008). The reweighting process underlying visual and physical (vestibular and proprioceptive systems) motion integration is a subadditive process in which the brain down-weights unreliable sensory stimuli while simultaneously up-weighting more reliable sensory stimuli.

The dorsal medial superior temporal cortex (MSTd) is thought to be the primary cortical area for the integration of visual and vestibular motion inputs and a possible site for the reweighting process (Morgan et al., 2008). Using single-cell recordings in macaques, Morgan et al. (2008) showed that the MSTd produces the greatest amount of activation related to self-motion from both visual (optic flow) and vestibular

(forward translations) motion stimuli. There is an advantage for multisensory presentations. When trained to discriminate between left and right translations provided by unisensory or multisensory cues, monkeys showed optimal perceptual sensitivity when visual and vestibular motion stimuli were combined as opposed to presented separately (Gu et al., 2008). This effect was not found when combined motion stimuli were spatially incongruent. MSTd contains separate clusters of neurons that respond optimally to either spatially congruent or incongruent presentations of visual and vestibular motion stimuli. Differences in activity of these cell types may play a role in parsing retinal image motion into self-motion versus motion from objects in the environment. If visual and vestibular motion stimuli are incongruent, it is likely that these inputs are being produced by separate events, such as seeing other objects move independently through the visual field during physical self-motion (Gu et al., 2008).

In humans, unisensory neuroimaging studies using visual self-motion have reported a variable set of cortical areas involved with self-motion

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processing including MSTd, parieto-insular vestibular cortex, medial temporal area (MT/V5), and ventral intraparietal area (Brandt et al., 1998; Palmisano et al., 2015). Although it is probable that self-motion processing is distributed across multiple brain areas, the findings of these studies are variable with respect to which areas show activation. One problem may be that some studies attempt to induce thevection illusion. The strength ofvection in individuals is difficult to measure objectively (for review, see Pitzalis et al., 2013). It is possible that the varying success ofvection induction between participants and studies may explain the inconsistencies in replicating localized brain activity (Palmisano et al., 2015). These neuroimaging studies have focused on visual stimuli to elicitvection because analysis of fMRI brain-imaging data is challenging when participants are in physical motion. Furthermore, presenting visual-motion stimuli in the absence of vestibular and proprioceptive stimuli can lead to sensory conflict when visual processing signals self-motion while proprioceptive and vestibular processing signals no self-motion (Campos and Bühlhoff, 2012). Incorporating both physical and visual motion would provide a more realistic and objective means to explore the multisensory nature of self-motion perception in humans.

Recent work has shown that electroencephalography (EEG) can be used successfully to record brain activation in a physically moving environment (Grundy et al., 2013; Nolan et al., 2012; Shedden et al., 2012; Townsend et al., 2015). EEG research has consistently shown that oscillations in the theta- (3–7 Hz), alpha- (8–12 Hz) and beta- (13–30 Hz) bands are associated with a variety of processes related to self-motion perception and motor function. Specifically, motor output has been associated with theta event-related synchronization (ERS; amplitude enhancement), and alpha and beta event-related desynchronization (ERD; blocking responses) (Pfurtscheller, 1992). Theta oscillations are diagnostic in spatial navigation and sensorimotor tasks for both human (Caplan et al., 2003) and non-human subjects (Koenig et al., 2011), and may be an index for a process that is critical for spatial computations such as forming cognitive maps (Koenig et al., 2011). Unisensory visual studies have shown greater alpha ERD in response to optic flow compared to static or spatially scrambled visual stimuli (Palmisano et al., 2016; Vilhelmsen et al., 2015). Changes in alpha ERD are also associated with other sensory modalities. During sensorimotor tasks, for example, alpha ERD is greater in motor regions compared to task-irrelevant brain areas (Pfurtscheller, 1992; Ofori et al., 2015). However, alpha ERD is more robust when induced by visual optic flow compared to flow from other sensory modalities (Klimesch et al., 2007). Beta ERD is induced by both active (Stancák and Pfurtscheller, 1996), and passive (Alegre et al., 2002), motor movements, suggesting that alpha and beta ERD index visual and motor processing, respectively. Coupled alpha- and beta-band ERD have been associated with multisensory body movements (Allen and MacKinnon, 2010; Cruikshank et al., 2012; Kilavik et al., 2013; McFarland et al., 2000; Ofori et al., 2015; Seeber et al., 2014). This observation further highlights the importance of observing responses to visual and physical motion together. Brain networks process multisensory inputs to self-motion, to the extent that unisensory self-motion cues may actually produce sensory conflict if motion is induced by one sense and not another (Campos and Bühlhoff, 2012).

Of interest to this study was whether observation of these oscillatory patterns may be diagnostic of self-motion perception during full-body accelerations through space, as is experienced while driving or flying. This type of experience can be simulated in driving and flight simulators with motion-based platforms. Over the past 30 years, there have been dramatic increases in both the research and application of motion-based simulator training in aviation and driving (for reviews see De Winter, Dodou & Mulder, 2012; Pinto et al., 2008). Recent research has begun exploring basic cognitive and sensory processes that play an underlying role in how humans perceive sensory cues provided by simulators (Eriksson, 2009). For example, several studies have shown that in multisensory simulated environments, attention to a specific modality can change behavior of the operator in several ways (Brickman et al.,

2000; Prewett et al., 2012).

There is a strong literature looking at integration of the visual, vestibular and proprioceptive systems, including age-related changes in multisensory integration that provide understanding of temporal and spatial windows within which optimal integration occurs (Ramkhalawansingh et al., 2018). Studies such as Butler et al. (2010), De Winkel et al. (2017), and Ohmi (1996), have used angular discrepancies between visual and vestibular cues (e.g. cue conflict) to measure relative cue weighting between the senses. This concept can be applied to flight and driving simulations, as drivers and pilots encounter visual-vestibular conflict when slowly accelerating or turning a vehicle (Ohmi, 1996). To avoid the costs of cue conflict, pilots and other operators of susceptible vehicles are often trained to discount physical cues to motion and attend to their visual instruments (Newman et al., 2012).

The goal of the present study was to examine whether attention to visual versus physical motion information would affect oscillatory power within the alpha, beta and theta ranges. Participants discriminated between left and right directions by attending to either visual or physical motion. Because beta ERD are more prevalent during active body movements, while alpha ERD are most robust during visual motion processing tasks, we hypothesized that allocating attention to physical motion stimuli would produce greater beta ERD and allocating attention to visual-motion stimuli would produce greater alpha ERD. Critically, our interest was in the modulation of these effects due to selection of one stimulus while ignoring another congruent or incongruent stimulus. We presented simultaneous visual and physical motion stimuli, which were either congruent or incongruent in direction. Incongruent cues to motion were incorporated to simulate visual-vestibular conflict. Using a directed attention task, we compared event-related spectral power (ERSP) during natural (congruent) motion conditions with conflicting (incongruent) conditions to observe whether cue congruency moderated ERSP.

2. Materials and methods

2.1. Participants

Thirty-seven participants (24 female) were recruited from the McMaster University psychology participant pool and the McMaster community. Ages ranged from 18 to 26 years ($M = 19$, $SD = 2.01$). Those recruited from the participant pool were compensated with course credits. All participants self-reported normal or corrected-to-normal visual acuity and reported no major problems with vertigo, motion sickness or claustrophobia. This experiment was approved by the Hamilton Integrated Research Ethics Board and complied with the Canadian tri-council policy on ethics.

2.1.1. Data and code availability

The data and code are available upon direct request of the corresponding author.

2.2. Stimuli

2.2.1. Visual motion stimuli

Visual-motion stimuli were presented on a 43-inch LCD panel 51 inches in front of the participant, subtending a visual angle of 41.23° . The panel had a resolution of 1920×1080 (1080p) and refresh rate of 60 Hz. At the beginning of each trial participants were presented with two yellow lines (tracks), demarking driving trajectories extending 35° of visual angle left and 35° right of center (see Fig. 1). To simulate a realistic driving environment, a blue sky with white clouds was displayed above the driving tracks. A fixation cross was presented at the center of the display for the entire trial. Visual motion consisted of a first-person view of moving forward along one of the yellow tracks. The timeline was forward left (or right) motion for 700 ms, followed by a 1200 ms pause at the end of the track, which signaled the end of the trial (1900 ms total). At the end of each trial the visual display was reset to the starting point of

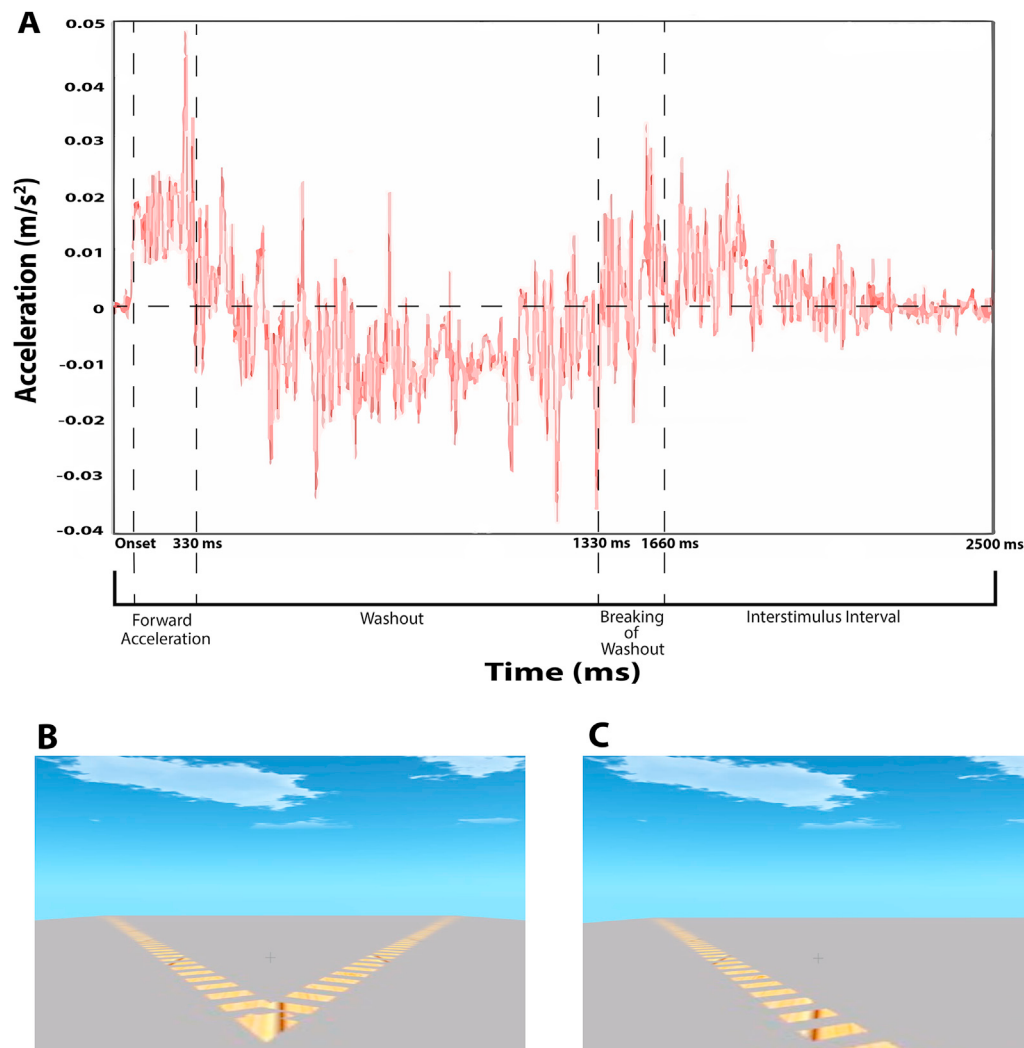


Fig. 1. Time course of physical- and visual-motion stimuli. Panel A shows an example of the profile of physical motion measured during a single trial by an accelerometer (red line); the variance shown is due to the high sensitivity of the accelerometer. The x-axis represents time and the y-axis represents acceleration ($g = m/s^2$). The acceleration profile is similar for 35° left and 35° right physical-motion trials. Panel B shows the visual display before motion onset; at this point the participant does not know whether visual motion will indicate travel along the left or right track. Panel C shows a still picture of the dynamic visual motion display at approximately 700 ms for a left visual motion trial.

the two yellow driving tracks.

2.3. Physical motion stimuli

A motion simulator provided physical-motion stimuli. The motion simulator pod was supported by a MOOG® platform with six-degrees-of-freedom motion (MOOG series 6DOF2000E; see [Inline Supplementary Figure A1](#)). Participants were seated in a bucket-style car seat fixed to the floor of the simulator pod. A button box was used for collecting behavioral responses, which participants held with their thumbs on color-coded buttons to make left/right responses. A camera mounted within the simulator was used to monitor participants throughout the experiment. Participants were provided with earplugs, and white audio noise was played inside the simulator in order to mask the sound of the motors.

Each physical-motion stimulus consisted of a forward linear translation at 35° left or right for 330 ms at 0.1 g (the longest our motion simulator could be moved given the spatial restrictions of the motion platform), followed by a corresponding washout for 1330 ms which returned the pod to the original position (1660 ms total). The acceleration intensity was selected based on preliminary testing to achieve a clear perception of forward motion within the spatial restrictions of the

movement of the platform while avoiding compensating movements of the head, neck or upper body. Physical forward accelerations were well above vestibular thresholds of 0.009 g as discussed by [Kingma \(2005\)](#). The motion force, $s(t)$, was described by:

$$s(t) = \begin{cases} A_1 & 0 \leq t \leq t_p \\ -A_2 & t_p \leq t \leq t_b \\ A_2 & t_b \leq t \leq t_e \\ 0 & \text{else} \end{cases}$$

where t represents time in seconds, t_p represents present time, t_b represents the breakpoint and t_e represents the end time. A_1 describes the initial forward acceleration, $-A_2$ describes the initial (backwards) acceleration of the washout, and A_2 describes the deceleration of the washout. Acceleration was measured using an Endevco accelerometer (model number 752A13), calibrated to approximately 1 mV/g sensitivity.

2.4. Experimental design and behavioral analyses

The present study had a 2 (Modality: Attend visual-motion vs. Attend physical-motion) x 2 (Congruency: Congruent [same direction] vs. Incongruent [opposing directions]) experimental design. To avoid task-

switching effects, the attend visual-motion (AV) and attend physical-motion (AP) conditions were separated into blocks. The task required participants to direct attention to either the visual-motion stimulus (attend visual or AV condition) or the physical-motion stimulus (attend physical or AP condition), and respond with a button press to indicate whether the direction of the relevant sensory motion was left or right. There was a practice AP block presented first, followed by 4 experiment blocks. During pilot testing we observed much lower accuracy for the incongruent AP trials in which participants had a difficult time ignoring the incongruent visual stimulus. Therefore, 3 of the 4 experimental blocks were AP compared to 1 AV block. This was done to ensure there would be enough correct trials in the incongruent AP condition for EEG analysis. The order of the 4 blocks was counterbalanced so that an equal number of participants received the AV block first, second, or third.

Within each block, 50% of trials were congruent (i.e., visual- and physical-motion stimuli signaled movement in the same direction, either left or right), and 50% were incongruent (i.e., visual-motion stimuli signaled motion to the left when physical-motion stimuli signaled movement to the right, and vice versa). Trial order was randomized within each block. Behavioral data were analyzed with two 2×2 repeated-measures ANOVAs for measures of judgment accuracy and response time.

2.5. Procedure

The entire session was between 1.5 and 2 h in duration. The timeline of the session included collection of demographic information (age, gender, and handedness; 5 min), followed by completion of one practice block (30 trials; 2 min), application of EEG electrodes (25 min), completion of four experimental blocks (199 trials each; 40 min), and clean up (40 min).

The timeline of each trial was as follows. The trial began with the visual display at the starting position of the two yellow tracks and the motion platform stationary at central position. The onset of visual- and physical-motion was simultaneous on each trial (see Fig. 1) signaling forward motion at an angle 35° to the left or right of center. A motion simulator is limited in that it is not possible to accelerate for an extended period of time due to mechanical limitations, but realistic perception of self-motion in a simulator is facilitated by the fact that the brain detects acceleration but not velocity. The physical- and visual-motion stimuli were synchronized as follows. The duration of the visual motion included 330 ms acceleration (to match physical motion acceleration) followed by 370 ms continued motion at the end velocity (700 ms). There was an additional 1200 ms delay at the end of the visual track (1900 ms). This corresponded to the 330 ms physical acceleration, a 1000 ms below threshold washout and a 330 ms breaking of the washout (1660 ms). Note that the initial 330 ms acceleration of the physical motion can be thought of as a ramp up to the end velocity; the visual motion was matched so that both are perceived to accelerate for 330 ms followed by a period of continued movement at the end velocity. Overall, each trial lasted 1900 ms, with the visual motion lasting 1900 ms and the physical motion lasting 1660 ms. The inter-trial interval was a random value between 1300 and 1500 ms, during which the motion platform remained at the central position.

To avoid excessive EEG artifacts due to eye movements and blinks, participants fixated on a central fixation cross during the trials and were provided with a blink break every 15 trials.

2.6. EEG data acquisition

EEG data were collected using the BioSemi ActiveTwo electrophysiological system (www.biosemi.com) with 128 sintered Ag/AgCl scalp electrodes. An additional four electrodes recorded eye movements (two placed laterally from the outer canthi and two below the eyes on the upper cheeks). Continuous signals were recorded using an open pass band from direct current to 150 Hz and digitized at 1024 Hz.

2.7. EEG preprocessing

All processing was performed in MATLAB-2014a using functions from EEGLAB (Delorme and Makeig, 2004) on the Shared Hierarchical Academic Research Computing Network (SHARCNET: www.sharcnet.ca). A flowchart illustrating the signal-processing pipeline can be found in the supplementary materials (see Inline Supplementary Figure A2). EEG data were band-pass filtered between 1 and 50 Hz, and epoched from 1000 ms pre-stimulus to 2000 ms post-stimulus. Each epoch was baseline corrected using the whole-epoch mean (Groppe et al., 2009). After referencing, channels with a standard deviation exceeding $200 \mu\text{V}$ were interpolated (on average, 0.5 channels interpolated per participant). Bad epochs were rejected if they had voltage spikes exceeding $500 \mu\text{V}$, or were rejected by EEGLAB's joint probability functions (Delorme et al., 2007).

Single-subject EEG data were submitted to an extended Adaptive Mixture Independent Component Analysis (AMICA) (Palmer et al., 2012) with an $N - (1 + \text{interpolated channels})$ Principal Components Analysis reduction. Decomposing an EEG signal into independent components (ICs) allows for analysis of each individual signal produced by the brain that would otherwise be indistinguishable (Desjardins and Segalowitz, 2013). Following AMICA, dipoles were fit to each IC using the fieldtrip plugin for EEGLAB (Oostenveld et al., 2011). ICs for which the dipole fit explained less than 85% of the weight variance, or whose dipoles were located outside the brain, were excluded from further analysis. On average, 5.2 ICs per subject were excluded from analysis.

2.8. ERSP Measure Projection Analysis

Event-related spectral power (ERSP) was computed for each of the remaining ICs. Fifty log-spaced frequencies between 3 and 50 Hz were computed, with 3 cycles per wavelet at the lowest frequency up to 25 at the highest. Measure Projection Analysis (MPA) was used to cluster ICs across participants using the Measure Projection Toolbox for MATLAB (Bigdely-Shamlo et al., 2013). MPA is a method of categorizing the location and consistency of EEG measures, such as ERSP, across single-subject data into 3D domains. These domains are subsets of ICs that are identified as having spatially similar dipole models, as well as similar ERSP activity (measure-similarity). MPA fits the selected ICs into a 3D brain model comprised of a cubic space grid with 8-mm spacing according to normalized Montreal Neurological Institute (MNI) space. Cortical regions of interest were identified by the MPA toolbox by incorporating the probabilistic atlas of human cortical structures provided by the Laboratory of Neuroimaging Project (Shattuck et al., 2008). Voxels that fell outside of the brain model (muscle artifacts, etc.) were excluded from the analysis.

We then calculated local convergence values, using an algorithm based on Bigdely-Shamlo et al. (2013) to deal with the multiple comparisons problem. Local convergence calculates the measure-similarity of dipoles within a given domain and compares them with randomized dipoles. In order to compare dipoles, a pairwise IC similarity matrix was created by estimating the signed mutual information between independent component-pair ERSP measure vectors, assuming a Gaussian distribution. As explained in detail by Bigdely-Shamlo et al. (2013), signed mutual information was estimated to improve the spatial smoothness of the obtained MPA significance value beyond determining similarity of dipoles through correlation. We used bootstrap statistics to obtain a significance threshold for convergence at each location of our 3D brain model. Following past literature, we set the raw voxel significance threshold to $p < .001$ (Bigdely-Shamlo et al., 2013; Chung et al., 2017).

For each domain calculated by MPA, ERSP was computed for each experimental condition. Within each domain, bootstrap statistics were used to assess differences in ERSP between conditions to uncover main effects of modality and congruency. Differences at each power band were computed by projecting the ERSP for each condition to each voxel in the domain. For each participant, this projection was weighted by dipole

density per voxel and then normalized by the total domain voxel density. Analysis of projected source measures were separated into discrete spatial domains by threshold-based Affinity Propagation clustering based on a similarity matrix of pair-wise correlations between ERSP measure values for each position. Following Chung et al. (2017), we used the maximal exemplar-pair similarity, which ranges from 0 to 10 to set a value of 0.8 (Bigdely-Shamlo et al., 2013; Chung et al., 2017; Ofori et al., 2015).

2.9. Stimulus validation

Perception of the onset of vestibular stimuli is a slower process than perception of the onset of visual stimuli (Barnett-Cowan and Harris, 2009, 2013). In our experiment, the onset and acceleration of movement of the physical and visual stimuli were synchronous to simulate a realistic experience. Because our interest was focused on performance based on selective attention when both physical and visual cues were present, it was important to make sure that the cues to motion in the two tasks (attend visual vs. attend physical motion) were equally salient. To this end, we collected a set of behavioral data prior to the EEG experiment to compare accuracy of responses to our visual- and physical-motion stimuli.

Twenty-one participants (12 female) were tested in two conditions. In the visual motion condition there was no physical motion; the simulator was parked. In the physical motion condition there was no visual motion; the yellow tracks were removed from the screen. All other aspects of the experiment were the same as the EEG experiment, including central fixation cross, timing parameters, and task. There was no difference in accuracy between visual- and physical-motion responses ($M = 99\%$ in both conditions), which supports the assumption that the salience of the physical-motion stimuli and the visual-motion stimuli were comparable in our experiment. Response time is not as diagnostic because we know that perception of physical motion is slower than visual motion (Barnett-Cowan and Harris, 2009). As expected, participants were slower to respond in the physical-motion condition ($M = 1212$ ms, $SE = 114.41$), than the visual-motion ($M = 933$ ms, $SE = 132.32$), condition, $t(20) = 3.76$, $p < .01$.

3. Results

We first analyzed accuracy and response times for the whole group. Based on the accuracy results, we identified two groups with differing abilities to ignore the prepotent visual motion information (high vs. low accuracy in the incongruent AP condition). We first present the whole group analysis (section 3.1). We then present a statistical comparison of the high and low accuracy groups (section 3.2). The focus of the remainder of the analyses is on the high-accuracy group (section 3.3).

3.1. Behavioral results for total sample

Initial 2×2 repeated-measures ANOVAs examined Modality (attend-visual vs. attend-physical) by Congruency (congruent vs. incongruent) for accuracy and response time. Participants were more accurate at discriminating direction in the attend-visual condition ($M = 99\%$, $SE = 0.17$) than the attend-physical condition ($M = 74\%$, $SE = 2.38$), $F(1, 42) = 117.65$, $p < .001$, $\eta_p^2 = 0.74$, and more accurate during congruent trials ($M = 96\%$, $SE = 0.47$) than incongruent trials ($M = 77\%$, $SE = 2.38$), $F(1, 42) = 61.34$, $p < .001$, $\eta_p^2 = 0.59$. There was a significant modality $\times$ congruency interaction $F(1, 42) = 62.48$, $p < .001$, $\eta_p^2 = 0.60$. Fisher's least significant difference (LSD) revealed that participants were significantly more accurate in the congruent attend-physical condition ($M = 93\%$, $SE = 0.94$) than the incongruent attend-physical condition ($M = 55\%$, $SE = 4.69$) ($p < .001$), however there was no significant difference in accuracy between the congruent ($M = 99\%$, $SE = 0.12$) and incongruent ($M = 99\%$, $SE = 0.25$) attend-visual conditions (see Table 1).

Participants were faster at discriminating direction in the attend-

visual condition ($M = 810$ ms, $SE = 49.67$) than the attend-physical condition ($M = 1257$ ms, $SE = 43.08$), $F(1, 42) = 111.39$, $p < .001$, $\eta_p^2 = 0.73$, and faster during congruent trials ($M = 1003$ ms, $SE = 42.06$) than incongruent trials ($M = 1065$ ms, $SE = 41.57$), $F(1, 42) = 27.33$, $p < .001$, $\eta_p^2 = 0.39$. There was a significant modality $\times$ congruency interaction $F(1, 42) = 22.30$, $p < .01$, $\eta_p^2 = 0.35$. LSD revealed that response times were significantly shorter in the congruent attend-physical condition ($M = 1199$ ms, $SE = 43.77$) than the incongruent attend-physical condition ($M = 1316$ ms, $SE = 45.24$) ($p < .001$), however there was no significant difference in response time between the congruent ($M = 807$ ms, $SE = 49.19$) and incongruent ($M = 814$ ms, $SE = 50.38$) attend-visual conditions. Table 1 shows mean accuracy and response times between conditions.

3.2. High-vs. low-accuracy group comparison

3.2.1. Behavioral results for high-vs. low-accuracy groups

Due to the large accuracy difference between the incongruent AP condition and the other conditions, we looked at the data from the incongruent AP condition more closely. Within this condition we observed accuracy differences that ranged between 5% and 93%. Further analysis indicated that some individuals were not successfully ignoring the incongruent visual motion when performing in the AP condition. To test this hypothesis we compared two groups created by selecting high- (>70% accuracy, $n = 16$) and low-accuracy (<30% accuracy, $n = 11$) participants based on accuracy in the incongruent AP condition. The remaining 10 participants were discarded for the high-vs. low-accuracy comparison.

It was not the case that low-accuracy participants were incorrectly attending to the visual motion instead of the physical motion in the incongruent AP condition. If they were, we would expect response times to be similar between the incongruent AV and incongruent AP conditions. However, a 2 (high-vs. low-accuracy groups) $\times$ 2 (Modalities: attend-visual vs. attend-physical) $\times$ 2 (Congruency: congruent vs. incongruent) mixed ANOVA showed that response times across all trials (correct and incorrect) did not differ between high- and low-accuracy groups. Response times were faster in the attend-visual condition ($M = 764$ ms, $SE = 66.53$) compared to the attend-physical condition ($M = 1125$ ms, $SE = 53.05$), $F(1, 23) = 37.38$, $p < .001$, $\eta_p^2 = 0.62$ for both high- and low-accuracy participants, suggesting that low-accuracy participants attempted to attend to the direction of the physical motion but failed to ignore the direction of the visual motion. This hypothesis is supported by the comparison of ERSP for high-vs. low-accuracy.

3.2.2. Oscillatory power (ERSP) for high-vs. low-accuracy groups

All domains identified by the Measure Projection Analysis (MPA) in both high- and low-accuracy participants are shown in Fig. 2. In Fig. 3 we

Table 1

Behavioral means. Accuracy (percent correct) and response times (ms) are shown for groups (high-accuracy [High], low-accuracy [Low] and all participants [All]), by conditions: congruent attend-visual (CAV), incongruent attend-visual (IAV), congruent attend-physical (CAP), and incongruent attend-physical (IAP). Standard errors are represented in brackets.

Accuracy (percent correct)				
	CAV	IAV	CAP	IAP
High	99 (0.60)	99 (0.69)	94 (0.88)	84 (1.30)
Low	99 (0.61)	98 (0.97)	95 (1.16)	12 (1.80)
All	99 (0.12)	99 (0.25)	93 (0.94)	55 (4.69)
Response times (ms)				
	CAV	IAV	CAP	IAP
High	788 (76)	815 (84)	1256 (64)	1341 (64)
Low	728 (101)	724 (111)	946 (85)	956 (85)
All	807 (49)	814 (50)	1199 (44)	1316 (45)

show the left motor areas of the high- and low-accuracy participants to provide a side-by-side comparison of how attending to a specific stimulus affected the ERSP activity in both groups. All ERSP is representative of a difference in oscillatory power compared to baseline (pre-trial) ERSP activity, where an ERS (event-related synchronization) represents more spectral power than baseline and an ERD (event-related desynchronization) represents less spectral power than baseline. We only show the left motor areas for the two groups because 1) the left motor area has the highest dipole density for both groups, and 2) there are no other MPA domains that have significant differences between conditions within the low-accuracy group (see Inline Supplementary Figures A3 and A4 for a complete MPA analysis of the low-accuracy participants). In Fig. 3, Panel A shows the left motor area in low-accuracy participants, which has the highest dipole density in dorsal posterior cingulate cortex (Brodmann area [BA] 31), and Panel D shows the left motor area in high-accuracy participants, which has the highest dipole density in somatosensory and primary motor cortex (BA 3 and 4). In Panels B, C (low-accuracy), E and F (high-accuracy) we show the associated ERSP plots for the congruent attend-physical (CAP) versus the congruent attend-visual (CAV), and incongruent attend-physical (IAP) versus the incongruent attend-visual (IAV) conditions. The ERSP plots are followed by bootstrapped comparisons between conditions for low- and high-accuracy participants within the left motor areas of both groups.

Theta-band activity: Comparing attend-visual with attend-physical in the congruent condition (CAV vs. CAP), the CAV condition elicited greater theta ERD ($p .05$) from ~ 500 ms to 600 ms post-stimulus compared to CAP in low-accuracy participants (Panel B). There were different findings in the theta band for high-accuracy participants. Comparing the CAV versus the CAP, the CAV condition elicited greater theta ERS from ~ 100 ms to 500 ms post-stimulus (Panel E). No differences in theta were found when comparing attend-visual with attend-physical in the incongruent condition (IAV vs. IAP) in low-accuracy

(Panel C) or high-accuracy participants (Panel F).

Alpha-band activity: Both low- and high-accuracy groups showed similar differences within the alpha-band when attending to visual vs. physical motion, but to different extents. For low-accuracy participants, the CAV condition elicited greater alpha ERD than CAP from stimulus onset to ~ 250 ms post-stimulus. This effect was due to an earlier onset of alpha ERD in the CAV condition (Panel B). When comparing IAV vs. IAP, there were no effects in the alpha band for low-accuracy participants (Panel C). High-accuracy participants showed a similar latency difference in alpha ERD but with more robust differences. Comparing the CAP versus the CAV, the CAV condition elicited greater alpha ERD ($p .05$) from stimulus onset to ~ 600 ms post stimulus than the CAP condition (Panel E). A similar effect was observed when comparing the IAP and IAV conditions; IAV elicited greater alpha ERD ($p .05$) from stimulus onset to ~ 600 ms post stimulus (Panel F).

Beta-band activity: For low-accuracy participants, the CAV condition elicited greater beta ERS than CAP from ~ 500 ms to ~ 1100 ms post-stimulus (Panel B), and similarly the IAV condition elicited greater beta ERS than IAP from ~ 600 ms to 1000 ms post-stimulus (Panel C). High-accuracy participants showed a different activity pattern in the beta band compared to low-accuracy participants. While attending to the physical motion, high-accuracy participants produced a longer lasting beta ERD that created more robust effects. The CAP condition elicited greater beta ERD than CAV from ~ 500 ms to the end of the trial (Panel E). The same effects was found when comparing IAV vs. IAP, the IAP condition elicited greater beta ERD from ~ 500 ms to the end of the trial (Panel F).

The data clearly show that attending to visual vs. physical motion stimuli elicited differences in spectral power within the high-accuracy participants. There were robust differences in theta, alpha and beta power between sensory modalities. In comparison, the low-accuracy participants showed minimal differences in spectral power between the

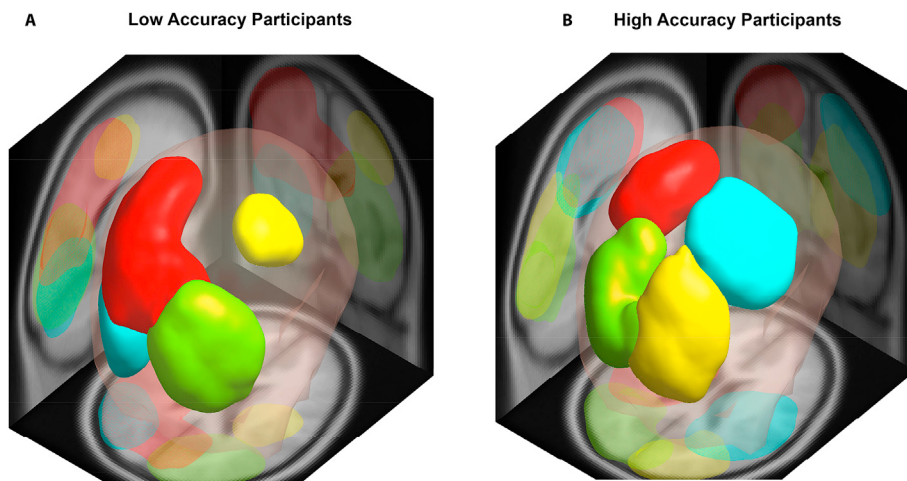


Fig. 2. MPA (Measure Projection Analysis) domains for low-accuracy and high-accuracy participants. Note that domains are ranked in terms of dipole density, with red being the densest, followed by green, blue and yellow respectively. Panel A shows a 3D representation of the brain model for low-accuracy participants. The red region represents the MPA domain with the greatest concentration of dipoles consistent with left dorsal posterior cingulate cortex (Brodmann area [BA] 31). The yellow region represents the MPA domain with the greatest concentration of dipoles consistent with right primary motor and primary somatosensory cortices (BA 4 and 3). The blue region represents the MPA domain with the greatest concentration of dipoles consistent with left associative visual and occipitotemporal area (BA 19 and 37). The green region represents the MPA domain with the greatest concentration of dipoles consistent with right secondary visual (V2), and associative visual (V3) areas (BA 18 and 19). Panel B shows a 3D representation of the brain for high-accuracy participants. The red region represents the MPA domain with the greatest concentration of dipoles consistent with left premotor and supplementary motor and primary motor cortex (BA 6 and 4). The blue region represents the MPA domain with the greatest concentration of dipoles consistent with right primary somatosensory and primary motor cortex (BA 3 and 4). The green region represents the MPA domain with the greatest concentration of dipoles consistent with left secondary visual (V2), and associative visual (V3) areas (BA 18 and 19). The yellow region represents the MPA domain with the greatest concentration of dipoles consistent with right secondary visual (V2), and associative visual (V3) areas (BA 18 and 19).

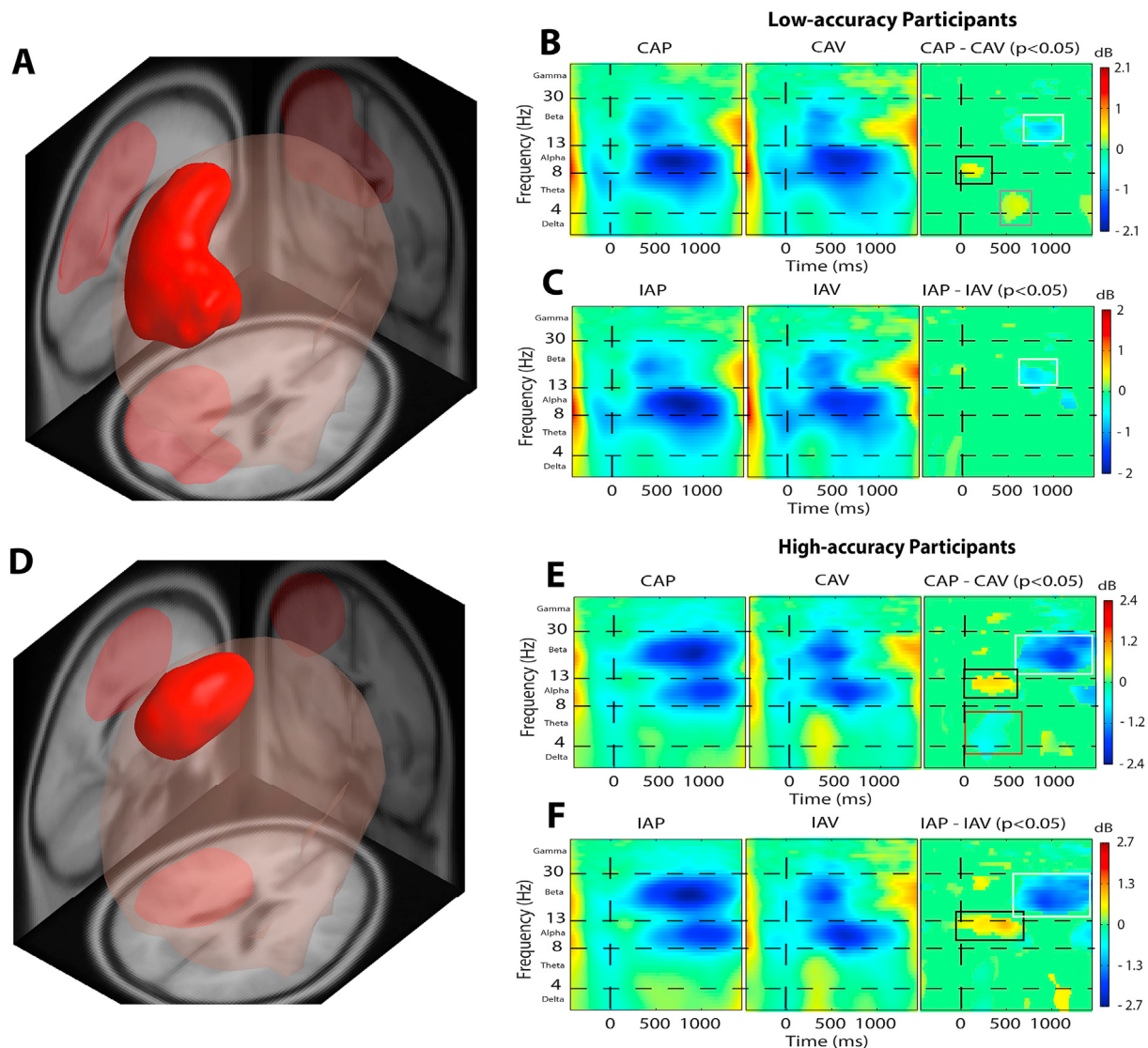


Fig. 3. Left motor areas identified by MPA and their respective ERS/ERD analysis for low-accuracy (Panels A, B, and C) and high-accuracy (Panels D, E, and F) participants. The ERS/ERD plots show time (ms) across the x-axis and frequency of the EEG signal along the y-axis. Panels B, C, E, and F show the associated ERS/ERD plots for the congruent and incongruent attend-physical (CAP, IAP) and attend-visual (CAV, IAV) conditions, and the bootstrapped comparisons ($p < .05$) between attend-physical and attend-visual conditions (CAP - CAV; IAP - IAV). ERS power is depicted in yellow/red, ERD power is depicted in blue, and green shows no difference in spectral power compared to baseline. **Low-accuracy participants:** Panel A shows a 3D representation of the brain model with the red region representing the MPA domain with the greatest concentration of dipoles consistent with left dorsal posterior cingulate cortex (BA 31). In Panel B, results of bootstrapped comparisons contrasting CAP with CAV are highlighted in the white square, showing significantly more beta ERD in the CAP condition. The black square highlights significantly more alpha ERD in the CAV condition (note that due to subtraction CAP-CAV, greater ERS power in CAP is represented in blue and greater ERD power in CAV is represented in yellow/red). The grey square highlights significantly more theta ERD in the CAV condition. Panel C: The white square highlights significantly more beta ERD in the IAP condition. **High-accuracy participants:** Panel D shows a 3D representation of the brain with the red region representing the MPA domain with the greatest concentration of dipoles consistent with left premotor and supplementary motor and primary motor cortex (BA 6 and 4) for high-accuracy participants. Panel E: The white square highlights significantly more beta ERD in the CAP condition. The black square highlights significantly more alpha ERD in the CAV condition. The brown square highlights significantly more theta ERS in the CAV condition. Panel F: The white square highlights significantly more beta ERD in the IAP condition. The black square highlights significantly more alpha ERD in the IAV condition.

same conditions. Moreover, these effects were only found in the left motor area; there were no differences between AP and AV conditions in the right motor area (see Appendix, Figure A3). There were also no congruency-related differences in the occipital regions within low-accuracy participants (see Inline Supplementary Figure A4). Even though low-accuracy participants were slower to respond when making heading judgments in the AP condition, their spectral power for the AP condition resembles the spectral power of the AV condition for both low- and high-accuracy participants. It is possible that these results reveal a bias towards greater weighting of visual-motion stimuli in low-accuracy participants. This bias could have potentially led to difficulties with

ignoring the incongruent visual stimulus, and thus low accuracy in the IAP condition.

Only data from the high-accuracy group were included for the remainder of the analyses.

3.3. Behavioral results for high-accuracy group

High-accuracy participants were analyzed separately to more effectively observe differences between successful responses in the attend-visual and attend-physical conditions.

3.3.1. Behavioral results (high-accuracy group)

Participants were more accurate at discriminating direction in the attend-visual condition ($M = 99\%$, $SE = 0.15$) than the attend-physical condition ($M = 88\%$, $SE = 1.29$), $F(1, 15) = 70.61$, $p < .001$, $\eta_p^2 = 0.83$, and more accurate during congruent trials ($M = 96\%$, $SE = 0.67$) than incongruent trials ($M = 91\%$, $SE = 0.91$), $F(1, 15) = 26.40$, $p < .001$, $\eta_p^2 = 0.64$. There was a significant modality $\times$ congruency interaction $F(1, 15) = 27.19$, $p < .001$, $\eta_p^2 = 0.64$. LSD revealed that participants were significantly more accurate in the congruent attend-physical condition ($M = 93.60\%$, $SE = 0.88$) than the incongruent attend-physical condition ($M = 84.14\%$, $SE = 1.30$) ($p < .01$), however there was no significant difference in accuracy between the congruent ($M = 99.59\%$, $SE = 0.60$) and incongruent ($M = 99.73\%$, $SE = 0.69$) attend-visual conditions (see Table 1).

Participants were faster at discriminating direction in the attend-visual condition ($M = 802$ ms, $SE = 87.05$) than the attend-physical condition ($M = 1286$ ms, $SE = 55.91$), $F(1, 15) = 38.89$, $p < .001$, $\eta_p^2 = 0.72$, and faster during congruent trials ($M = 1012$ ms, $SE = 60.78$) than incongruent trials ($M = 1076$ ms, $SE = 63.78$), $F(1, 15) = 30.05$, $p < .001$, $\eta_p^2 = 0.67$. There was a significant modality $\times$ congruency interaction $F(1, 15) = 15.02$, $p < .01$, $\eta_p^2 = 0.50$. LSD revealed that response times were significantly shorter in the congruent attend-physical condition ($M = 1256$ ms, $SE = 63.72$) than the incongruent attend-physical condition ($M = 1341$ ms, $SE = 64.10$) ($p < .01$), however there was no significant difference in response time between the congruent ($M = 788$ ms, $SE = 76.39$) and incongruent ($M = 815$ ms, $SE = 83.60$) attend-visual conditions. Table 1 shows mean accuracy and response times between conditions.

3.3.2. Oscillatory power (ERSP) for high-accuracy group

In Fig. 4 we show the left and right motor areas of the high-accuracy participants to provide a side-by-side comparison of how attending to a specific stimulus affected the ERSP activity in both MPA domains. These were the only two domains that showed a significant main effect of modality. In Fig. 4, Panel A shows the left premotor and supplementary motor and primary motor cortex (BA 6 and 4), and Panel D shows the right motor area, consistent with the somatosensory and primary motor cortex (BA 3 and 4). In Panels B, C (left motor), E and F (right motor) we show the associated ERSP plots for the congruent attend-physical (CAP) versus the congruent attend-visual (CAV), and incongruent attend-physical (IAP) versus the incongruent attend-visual (IAV) conditions. The ERSP plots are followed by bootstrapped comparisons between conditions for left and right motor areas.

Theta-band activity: Comparing CAV versus CAP, the CAV condition elicited greater theta ERS ($p .05$) from ~ 100 ms to 500 ms post-stimulus compared to CAP in the left motor area (Panel B). There were different findings in the theta band for the right motor area. Comparing the CAV versus the CAP, the CAP condition elicited greater theta ERS from ~ 600 ms to ~ 1000 ms post-stimulus (Panel E). No differences in theta were found when comparing attend-visual with attend-physical in the incongruent condition (IAV vs. IAP) in the left motor (Panel C), however, in the right motor area, IAP elicited greater theta ERS from ~ 600 ms to ~ 1000 ms post-stimulus than IAV (Panel F).

Alpha-band activity: Both left and right motor areas showed similar differences within the alpha-band when attending to visual vs. physical motion. For the left motor area, the CAV condition elicited greater alpha ERD ($p .05$) from stimulus onset to ~ 600 ms post stimulus than the CAP condition (Panel B). Comparing the CAP versus the CAV in the right motor area, the CAV condition elicited greater alpha ERD ($p .05$) from stimulus onset to ~ 200 ms post stimulus than the CAP condition (Panel E). When comparing IAV vs. IAP, both the left and right motor areas showed greater alpha ERD from stimulus onset to ~ 600 ms post stimulus (Panels C and F).

Beta-band activity: Differences in beta-band activity were the same for each comparison. When comparing CAV versus CAP (Panels B and E), and IAV versus IAP (Panels C and F), the AP conditions elicited greater

beta ERD ($p .05$) from ~ 600 ms to 1500 ms post-stimulus in both the left and right motor areas.

In Fig. 5 we show the left and right occipital areas of the high-accuracy participants to provide a side-by-side comparison of how stimulus congruency affected the ERSP activity in both MPA domains. These were the only two domains that showed a significant main effect of congruency. In Fig. 5, Panel A shows the left occipital area that is consistent with the secondary visual (V2), and associative visual (V3) areas (BA 18 and 19), and Panel D shows the right occipital area, also consistent with the secondary visual (V2), and associative visual (V3) areas (BA 18 and 19). In Panels B, C (left occipital), E and F (right occipital) we show the associated ERSP plots for the incongruent attend-physical (IAP) versus the congruent attend-physical (CAP), and incongruent attend-visual (IAV) versus the congruent attend-visual (CAV) conditions. The ERSP plots are followed by bootstrapped comparisons between conditions for left and right occipital areas.

Theta-band activity: Comparing IAP versus CAP, the IAP condition elicited greater theta ERD ($p .05$) from ~ 100 ms to 500 ms post-stimulus compared to CAP in the left occipital area (Panel B). Congruency did not elicit any ERSP differences in any other MPA domain (Panels C, E and F).

4. Discussion

We present the first high-density electrophysiological study to explore the effects of attention and congruency on the perception of multisensory self-motion. We combined visual- and physical-motion stimuli in a direction discrimination task in which attention was directed either to visual- or physical-motion cues. The direction of self-motion in the attended modality was either congruent or incongruent with the direction of self-motion in the ignored modality.

We were able to compare ERSP in the conditions with conflicting motion cues to ERSP in the congruent self-motion conditions and observe oscillatory differences elicited by attending to one motion cue and ignoring the other.

4.1. Beta oscillations in physical motion processing

The time-course of beta oscillations during motor output has drawn attention over the past several decades (for review see Kilavik et al., 2013). During static hold (holding a single posture), beta oscillations show an increase in power about 300 ms after stabilization following the beta ERD elicited by the movement that produced the form of the given posture. The time period leading up to a movement that terminates the static hold (planning the movement) is characterized by a gradual decrease in beta power, reaching a peak ERD at movement onset. This pre-movement beta ERD may be modulated by uncertainty about the direction of the forthcoming movement (Tzagarakis et al., 2010). For example, using an instructed-delay reaching task with one or multiple possible target directions, Tzagarakis et al. (2010) demonstrated that the pre-movement beta ERD was greater if the participant was uncertain of the required direction of movement during the pre-movement phase of the task.

Consistent with these time-course studies, beta ERD is strongest during movement execution and during changes in isometric muscle contraction (Alegre et al., 2002; Ofori et al., 2015; Tzagarakis et al., 2010). It lasts until the movement is complete, and is typically observed bilaterally over sensorimotor areas (Salmelin and Hari, 1994; Stancák and Pfurtscheller, 1996). Beta power rapidly increases if movement is not performed, for example after presentation of a No-Go signal (Alegre et al., 2004), or as soon as the muscle contraction or posture stabilizes (Baker et al., 1999). This increase in beta power following the offset of movement is known as beta rebound, and it typically occurs 300–1000 ms post-movement (for review see Kilavik et al., 2013). The power of the beta rebound seems to parallel the speed of the preceding movement (Parkes et al., 2006), although some investigators have reported no difference between varying speeds of movements (Stancák and

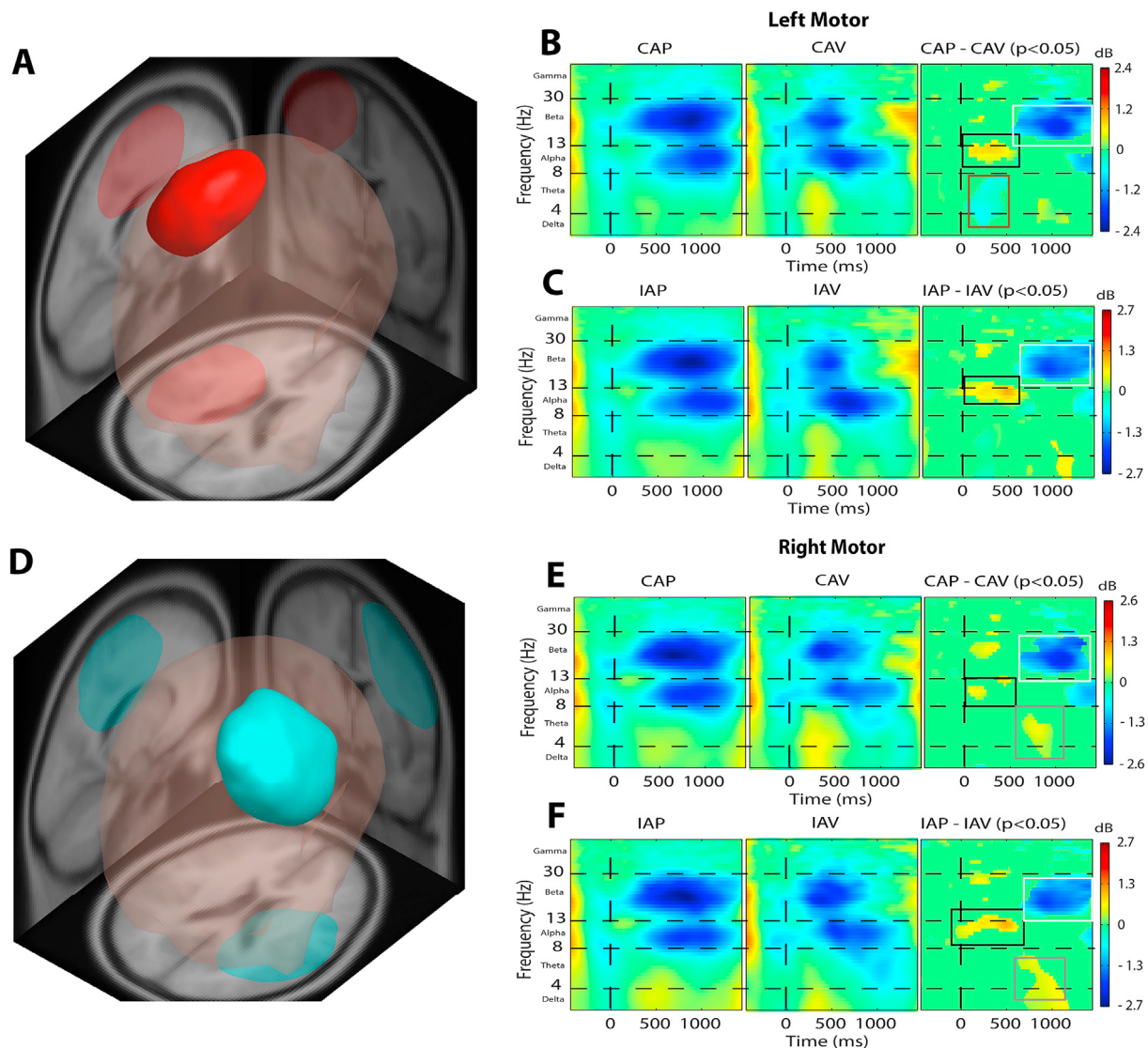


Fig. 4. Left (Panels A, B, and C) and right (Panels D, E, and F) motor area identified by MPA and respective ERSP analysis in high-accuracy participants. The ERSP plots show time (ms) across the x-axis and frequency of the EEG signal along the y-axis. Panels B, C, E, and F show the associated ERSP plots for the congruent and incongruent attend-physical (CAP, IAP) and attend-visual (CAV, IAV) conditions, and the bootstrapped comparisons ($p < .05$) between attend-physical and attend-visual conditions (CAP – CAV; IAP – IAV). **Left motor area:** Panel A shows a 3D representation of the brain with the red region representing the MPA domain with the greatest concentration of dipoles consistent with left premotor and supplementary motor and primary motor cortex (BA 6 and 4). Panel B: Results of bootstrapped comparisons contrasting CAP with CAV are highlighted in the white square, showing significantly more beta ERD in the CAP condition. The black square highlights significantly more alpha ERD in the CAV condition (note that due to subtraction CAP-CAV, greater ERS power in CAV is represented in blue and greater IERD power in CAV is represented in yellow/red). The brown square highlights significantly more theta ERS in the CAV condition. Panel C: The white square highlights significantly more beta ERD in the IAP condition. The black square highlights significantly more alpha ERD in the IAV condition. **Right motor area:** Panel D shows a 3D representation of the brain with the blue region representing the MPA domain with the greatest concentration of dipoles consistent with right primary somatosensory and primary motor cortex (BA 3 and 4). Panel E: The white square highlights significantly more beta ERD in the CAP condition. The black square highlights significantly more alpha ERD in the CAV condition. The grey square highlights significantly more theta ERS in the CAP condition. Panel F: The white square highlights significantly more beta ERD in the IAP condition. The black square highlights significantly more alpha ERD in the IAV condition. The grey square highlights significantly more theta ERS in the CAP condition.

Pfurtscheller, 1996). Similar to the motor imagery beta ERD described by Nakagawa et al. (2011), the beta rebound has also been demonstrated in motor imagery tasks (Solis-Escalante et al., 2012). A hypothesis proposed by Gaetz and Cheyne (2006), is that the function of beta rebound may be to recalibrate or reset the motor system to new conditions, in order to prepare for a subsequent movement. After the onset of beta rebound, the beta oscillation cycle begins again with the preparation for a new movement.

The present study observed this bilateral beta ERD after stimulus onset regardless of the attentional requirements of the condition or high versus low accuracy group. This finding is not surprising, as each

condition delivered identical physical motion stimuli. In high-accuracy participants, there were no significant differences in beta ERD between the attend-physical and attend-visual conditions until 600 ms post-stimulus. Beginning at about 600 ms post-stimulus, a higher amplitude beta ERD was found in the motor areas when participants attended to physical-vs. visual-motion stimuli. The only difference between the attend-physical and attend-visual conditions was an instruction difference in which participants were informed which sensory modality to attend (i.e. the motion stimuli were identical), so the difference in beta ERD is unlikely to be due to sensory stimuli alone. We believe this finding reflects increased and longer lasting motor processing because attending

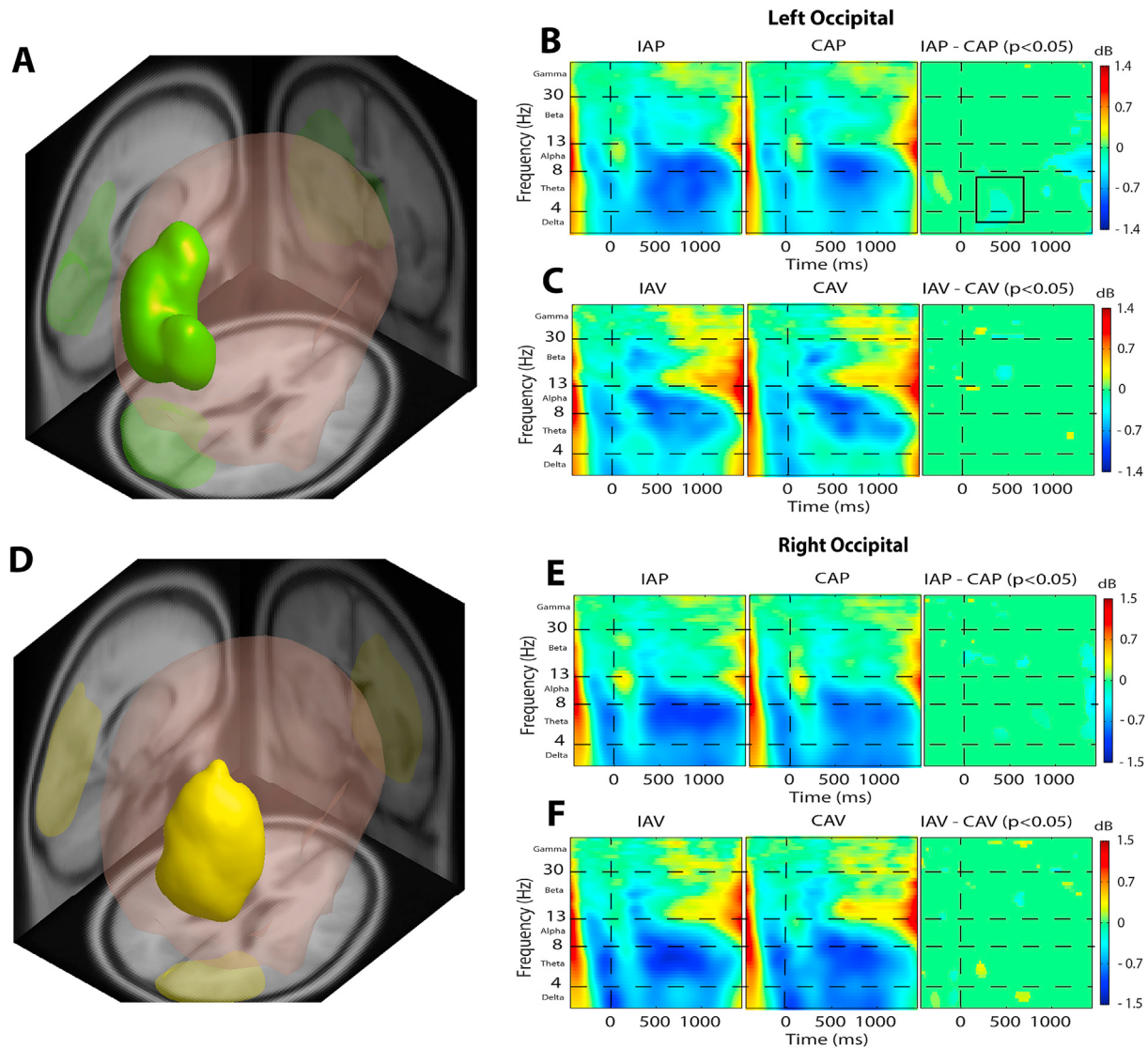


Fig. 5. Left (Panels A, B, and C) and right (Panels D, E, and F) occipital area identified by MPA and respective ERSP analysis in high-accuracy participants. The ERSP plots show time (ms) across the x-axis and frequency of the EEG signal along the y-axis. Panels B, C, E, and F show the associated ERSP plots for the incongruent and congruent attend-physical (IAP, CAP) and attend-visual (IAV, CAV) conditions, and the bootstrapped comparisons ($p < .05$) between incongruent and congruent conditions (IAP - CAP; IAV - CAV). ERS power is depicted in yellow/red, ERD power is depicted in blue, and green shows no difference in spectral power compared to baseline. **Left occipital area:** Panel A shows a 3D representation of the brain with the green region representing the MPA domain with the greatest concentration of dipoles consistent with left secondary visual (V2), and associative visual (V3) areas (BA 18 and 19). Panel B: Results of bootstrapped comparisons comparing IAP with CAP are highlighted in the black square, showing significantly more theta ERD in the IAP condition. Panel C: There are no significant effects of congruency. **Right occipital area:** Panel D shows a 3D representation of the brain with the yellow region representing the MPA domain with the greatest concentration of dipoles consistent with right secondary visual (V2), and associative visual (V3) areas (BA 18 and 19). Panel E and F: There are no significant effects of congruency.

to the physical-motion information is more difficult than attending to the visual-motion information. Moreover, in high-accuracy participants, there was a significant difference in beta power at an even later stage (>1000 ms post-stimulus). This can be described as follows. As described above, a large beta ERD was observed beginning about 600 ms in both the attend-physical condition and the attend-visual condition. When participants attended the physical motion, the beta ERD maintained until the end of the trial. In contrast, when participants attended the visual motion, there was a noticeable beta ERS (beta rebound) beginning around 1000 ms (see Fig. 4). There may be two possible explanations for this difference in beta power between the attend-physical and attend-visual conditions. If observation of beta rebound reflects termination of motion output (Kilavik et al., 2013), it may be that sustained attention to the physical motion suppressed the beta rebound. This hypothesis would support motor imagery studies that show beta ERD can be elicited by a top-down activation of the motor area entirely through attention, in the

absence of physical motion (Nakagawa et al., 2011; Koelewijn et al., 2008). In our experiment the motion simulator was completing the washout phase during the beta rebound, which may still be consistent with the hypothesis mentioned above, in which the function of beta rebound recalibrates the motor system to new conditions (Gaetz and Cheyne, 2006). However, in that case we would expect to observe beta rebound in both attention conditions. Alternatively, the observation of beta rebound in the attend-visual condition, when attention was directed to the visual motion, might be part of a mechanism to suppress the ignored physical motion processing. Considering that the integration of the visual and vestibular systems is a subadditive process (Angelaki et al., 2009; Morgan et al., 2008), this robust beta ERS (beta rebound) might reflect an inhibitory process during visual-vestibular integration in which visual motion is weighted greater than vestibular motion.

Low-accuracy participants did not show the same differences in beta oscillatory power between modalities. Although they showed slight

modality differences in beta oscillations in the left motor cortex, the differences were minimal and were not found in any other MPA domain. It is possible that the difference between high- and low-accuracy participants is that the low-accuracy participants attended to the visual motion stimuli, regardless of whether the condition required visual or vestibular attention. We propose, however, that since low-accuracy participants responded significantly slower during the attend-physical condition, that they were at least attempting to attend to the physical motion. We suggest that low-accuracy participants had difficulties inhibiting the processing of the visual motion during the attend-physical condition, which led to poor performance in the incongruent attend-physical condition. We observed beta ERD for about 700 ms followed by a beta ERS in every condition with the low-accuracy participants. If we are correct and low-accuracy participants have difficulty inhibiting visual processing, our finding supports the hypothesis that the beta rebound might be part of a mechanism to inhibit physical-motion processing during visual-vestibular integration.

4.2. Alpha oscillations in motor processing

Alpha ERD has been associated with high focal cortical activation, while alpha ERS has been associated with deactivation or inhibition, particularly within task-irrelevant brain areas (Klimesch, 2012). For example, Foxe et al. (1998) presented participants with audio-visual stimuli in a multisensory selective attention paradigm. They showed alpha ERD over parieto-occipital sites (associated with visual attention) during an attend-visual condition, while the uninvolved brain regions showed alpha ERS. Conversely, they found alpha ERS in the parieto-occipital area induced by the same stimuli during an attend-auditory condition. This oscillatory alpha pattern has also been shown in the motor cortex when Pfurtscheller (1992) observed alpha ERD during execution of hand motor tasks. In the same experiment, during visual tasks, Pfurtscheller (1992) observed alpha ERD at posterior-parietal areas (non-motor) and alpha ERS over hand motor regions. However, it should be noted that alpha ERD in task-relevant brain areas tends to have the greatest power in visual tasks compared to other sensory modalities (Klimesch et al., 2007).

Alpha ERD can also be evoked by the onset of visual motion stimuli (Vilhelmsen et al., 2015). This association was demonstrated by Vilhelmsen et al. (2015) when participants passively viewed an optic flow pattern consisting of a virtual road with poles at both sides to enhance the subjective experience of visual forward motion. Three conditions consisted of different driving speeds (25, 50, and 75 km/h) followed by a static control condition. Vilhelmsen et al. (2015) found alpha ERD in the visual-motion conditions compared to alpha ERS in the static control within the midline parietal region. No differences in alpha power were found between motion speeds.

The present study found robust alpha ERD in every condition within the left and right motor and occipital regions. The alpha ERD within occipital regions was not modulated by the attended modality, or stimulus congruency, so the discussion of alpha power is restricted to motor regions. We found significantly greater alpha ERD (between 0 and 600 ms) in both motor cortices (there were no lateralized effects) when participants attended to visual motion compared to physical motion. This is likely due to the fact that in the attend-visual condition, alpha ERD began at stimulus onset, whereas in the attend-physical condition the induced alpha ERD had a later onset (~450 ms post-stimulus). This latency difference between conditions produces the alpha ERD differences shown in the subtraction boxes of Fig. 4. Others have demonstrated that the motor regions produce alpha ERD during processing of both visual and physical motor output when presented separately (Vilhelmsen et al., 2015; Pfurtscheller, 1992; Ofori et al., 2015). The alpha ERD latency difference in the attend-visual versus attend-physical conditions in our experiment likely represents an attentional effect on cortical activation associated with different processes (i.e. visual and physical motion processing). This latency hypothesis is consistent with Barnett-Cowan and

Harris (2009) who demonstrated that perception of visual versus vestibular information has different time-courses.

It is also possible that the latency of alpha ERD is diagnostic of individual differences in the way that the visual- and physical-motion cues are being processed when participants are asked to distinguish between them during simultaneous presentation. Low-accuracy participants produced alpha ERD at visual stimulus onset regardless of whether they were attending to visual or physical motion, and these participants performed poorly in the attend-physical condition when attempting to ignore incongruent visual motion cues. We believe this is further evidence to support our hypothesis that latency of alpha ERD is diagnostic of which modality is being processed. In other words, the low-accuracy participants found great difficulty in ignoring the visual motion information and this was reflected in the latency of alpha ERD.

4.3. Theta oscillations in sensorimotor integration

Theta oscillations have long been studied in relation to spatial navigation in the hippocampus of the rat (Grastyan et al., 1966; O'keefe and Conway, 1978). They have been shown to be correlated with complex spatial behaviors such as exploring (Grastyan et al., 1966), and forming cognitive maps (O'keefe and Conway, 1978). More recently, Bland (2009) proposed an alternate model where theta oscillations facilitate integration between the sensory and motor systems. The model states that the hippocampus and associated areas use theta oscillations to provide sensory and motor systems with a feedback loop to update one another on their performance relative to dynamic changes in the sensory environment. The model was developed to explain sensorimotor integration in rats but has since been applied to human behavior (Caplan et al., 2003; Cruikshank et al., 2012). In an instructed delayed reaching paradigm, Cruikshank et al. (2012) asked participants to press and hold a button to begin each trial, which was then followed by the presentation of a black dot on a touch screen in front of them. Shortly after the presentation of the dot, an auditory tone sounded and, under two conditions, participants were required to release the button and touch the area of the screen where the dot was presented. In condition 1, the dot disappeared as soon as the button was released (movement onset), and in condition 2 the dot disappeared simultaneously with the tone (before movement onset). This paradigm required that participants integrate visuo-spatial information about the dot in order to coordinate a goal-directed movement. Cruikshank et al. (2012) found greater theta ERS during movement initiation and execution than during periods of stillness. They also found greater theta ERS over temporal sites during response initiation in condition 2 than in condition 1. Note that condition 2 requires greater integration and planning compared to condition 1. They propose that this is evidence of sensorimotor integration based on converging evidence that perceptual brain mechanisms in the ventral stream of the visual system are engaged when planning perceptually driven hand movements. For example, increased theta power has been shown during the planning phases of a catching task (Tombini et al., 2009), during the planning and execution phases of a choice-reaction task (Perfetti et al., 2010), and during motor imagery for sensorimotor planning (Hinterberger et al., 2008). Cruikshank et al. (2012) did not find differences in theta ERS between conditions at any other electrode sites, suggesting that this temporal theta ERS was task-specific to the preparation of the reaching.

The present study prompted simpler spatial behaviors than Cruikshank et al. (2012) yet still required sensorimotor integration, and still found robust differences in theta power. Differences in theta power were elicited by manipulations in both the attended modalities and congruency of the visual and physical self-motion cues. We found different patterns of theta power when comparing the attend-physical vs. the attend-visual conditions. In the attend-visual condition we found a powerful but brief theta ERS between stimulus onset and 500 ms post-stimulus, followed by a return to baseline. Whereas in the attend-physical condition we found less powerful but longer-lasting theta

ERS beginning from around 200 ms post-stimulus and lasting until the end of the trial. The subtraction boxes in Fig. 4 show that theta ERS is significantly greater between stimulus onset and 500 ms post-stimulus during attend-visual trials (specifically in the left motor area). During attend-physical trials, theta ERS is significantly greater from around 500 ms post-stimulus to 1000 ms post-stimulus (specifically in the right motor area) compared to attend-visual trials. Differences in theta may reflect the different processing demands required when attending to the different sensorimotor stimuli. The brief but powerful theta burst in the attend-visual condition may reflect fast processing at stimulus onset and a cessation of processing of the visual-motion cue after the appropriate response had been determined. The long-lasting theta ERS during the attend-physical condition may reflect more extended processing of the physical-motion stimulus, which we know has a slower perceptual response (Barnett-Cowan and Harris, 2009).

We also found that incongruent attend-physical trials elicited greater theta ERD than congruent attend-physical trials. This main effect was found around 100 ms and lasted to 500 ms post-stimulus in the left occipital area. This effect was only found while participants attended to physical motion stimuli, and not in the attend-visual condition, and was only shown in the left occipital area. It is likely that we did not find this effect in the incongruent attend-visual condition because the physical-motion stimuli in this experiment were less salient and thus less challenging for the participant to ignore than the visual-motion stimuli. Participants likely dealt with more interference from incongruent visual stimuli in the attend-physical condition.

We believe that this decrease in theta power may be due to the breaking of sensorimotor integration when self-motion cues are incongruent. We did not find any effect of congruency within our low-accuracy participants in any MPA domain, which is likely due to the fact that they had great difficulty ignoring the visual stimuli, and thus may not have noticed the spatial mismatch. This pattern of theta ERD in response to incongruent self-motion stimuli may be the neural response to visual-vestibular conflict.

4.4. Limitations of the present study

There are two limitations of the present study that are important to discuss. Both attend-visual and attend-physical conditions required participants to fixate on a central fixation cross. This is an important part of the design of the EEG experiment to reduce the contribution of eye-movement artifacts. However, one might argue that this set up an unequal comparison between the two conditions because the visual fixation was the same modality as the target motion in the attend-visual condition but was a different modality as the target motion in the attend-physical condition. We acknowledge that it is possible that processing was affected by the requirement to fixate. However, we know that it is possible to disassociate eye movements and attention (e.g. Posner, 1980; Ramkhalawansingh et al., 2018), especially when the information at fixation is not task relevant, which may help to reduce concerns about the impact of the fixation requirement.

The second limitation relates to the relatively poor spatial resolution of EEG data compared to other brain-imaging methods such as fMRI and PET. It is wise to be cautious about attributing brain activity to specific brain regions using EEG. The IC dipoles clustered via MPA have an associated probability of membership to a brain domain (Acar & Makeig, 2013).

5. Conclusion

The present study is the first to use EEG to explore the effects of attention and cue congruency while participants are presented with simultaneous visual and physical self-motion stimuli. There were three main findings. 1) There was a difference in theta power between congruent and incongruent trials in the left occipital area when participants completed the attend-physical condition. Incongruent trials elicited

a more robust theta ERD than congruent trials. Theta power is commonly associated with sensorimotor integration and this robust congruency difference may be due to a breaking of integration. It may be that this theta power difference only occurs while attending to physical motion because in this experiment, the visual motion stimuli were more salient, thus more disruptive during integration when it was incongruent with the physical-motion cue. We believe the difference in theta due to congruency may reflect a neural response to visual-vestibular conflict. 2) Alpha, beta and theta power in the motor areas were shown to change when participants attended to a specified stimulus while simultaneously ignoring the other. There were more powerful alpha and beta ERD and less powerful and later onset of theta ERS while participants attended to the physical motion. Previous research has demonstrated all three frequencies in the motor areas during unisensory visual- and physical-movement tasks. We have demonstrated that these power/latency differences are reflective of attentional allocation considering the stimuli in both attentional conditions were identical. 3) Participants who performed at thirty percent accuracy or less on the incongruent attend-physical condition showed a minimal difference in alpha, beta and theta oscillations between the attend-visual and attend-physical conditions but only in the left motor cortex. Significant differences in oscillatory power were not found in any other MPA domain for the low-accuracy participants despite response times being significantly slower in the attend-physical than the attend-visual conditions. The ERSP of low-accuracy participants in both sensory modalities closely resembled the ERSP of high-accuracy participants during the attend-visual condition. These null results may reflect a greater visual bias for the low-accuracy participants, which would explain the relatively low accuracy (12%) during the incongruent attend-physical condition but high accuracy (95%) for the congruent attend-physical condition. To our knowledge, this is the first study to explore neural oscillations associated with visual-vestibular conflict. Further research is required to understand the nature of this theta ERD and exactly how it relates to the sensorimotor integration loop proposed by Bland (2009).

Conflicts of interest

The authors declare no competing financial interests. Funding for this study was provided to JMS and MvM by The Natural Sciences and Engineering Research Council of Canada (RGPGP-2014-00051); and the Canada Foundation for Innovation (2009M00034). These funding sources had no involvement in the study design, the collection, analysis and interpretation of data, in the writing of the report, and in the decision to submit the article for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2019.02.015>.

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