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Dissociation of frontal-midline delta-theta and posterior alpha oscillations: A mobile EEG study

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Abstract

Numerous reports have demonstrated low-frequency oscillations during navigation using invasive recordings in the hippocampus of both rats and human patients. Given evidence, in some cases, of low-frequency synchronization between midline cortex and hippocampus, it is also possible that low-frequency movement-related oscillations manifest in healthy human neocortex. However, this possibility remains largely unexplored, in part due to the difficulties of coupling free ambulation and effective scalp EEG recordings. In the current study, participants freely ambulated on an omnidirectional treadmill and explored an immersive virtual reality city rendered on a head-mounted display while undergoing simultaneous wireless scalp EEG recordings. We found that frontal-midline (FM) delta-theta (2–7.21 Hz) oscillations increased during movement compared to standing still periods, consistent with a role in navigation. In contrast, posterior alpha (8.32–12.76 Hz) oscillations were suppressed in the presence of visual input, independent of movement. Our findings suggest that FM delta-theta and posterior alpha oscillations arise at independent frequencies, under complementary behavioral conditions, and, at least for FM delta-theta oscillations, at independent recordings sites. Together, our findings support a double dissociation between movement-related FM delta-theta and resting-related posterior alpha oscillations. Our study thus provides novel evidence that FM delta-theta oscillations arise, in part, from real-world ambulation, and are functionally independent from posterior alpha oscillations.

KEYWORDS
BOSC, EEG, spatial navigation, theta, virtual reality

1 | INTRODUCTION

Vanderwolf first reported increases in low-frequency oscillations in the EEG of the rat hippocampus and cortex during ambulation (Vanderwolf, 1969), suggesting a link between low-frequency oscillations and movement. Later human studies confirmed such an association using invasive depth electrode recordings in human epilepsy patients. These reports showed that hippocampal and, to a lesser extent, cortical low-frequency oscillations within the delta, theta, and alpha bands (1–12 Hz), increased during movement in both real world and virtual reality in human patients (Bohbot, Copara, Gotman, & Ekstrom, 2017; Caplan et al., 2003; Ekstrom

et al., 2005; Watrous, Fried, & Ekstrom, 2011) and that the duration of such hippocampal oscillations coded the spatial distance travelled (Bush et al., 2017; Vass et al., 2016). There are some important limitations with these studies, however. First, they involved epilepsy patients with implanted electrodes, and interictal discharge (activity between seizures) may impact how these oscillations manifest (Blumenfeld et al., 2004). Second, they focused primarily on the hippocampus or other deep cortical structures difficult to access with scalp EEG. Third, many of these studies involved desktop virtual reality and thus limited ambulation. One unexplored possibility is that low-frequency movement-related oscillations also manifest in healthy

PSYCHOPHYSIOLOGY SPR

human neocortex; thus, one suggestion to help reconcile the above limitations is to investigate frontal-midline theta (FM theta) oscillations using scalp EEG in healthy participants freely ambulating.

Although previous studies have used noninvasive neuroimaging to investigate the electrophysiological correlates of spatial navigation (de Araújo, Baffa, & Wakai, 2002; Kaplan et al., 2012, 2017; Snider, Plank, Lynch, Halgren, & Poizner, 2013; Weidemann, Mollison, & Kahana, 2009), free ambulation was not incorporated in the experimental design because of the difficulties of coupling effective neuroimaging and unrestrained, body-based movement. For example, in conventional scalp EEG recordings, data transmission cables connecting the sensors and amplifiers intrinsically limit the distance participants can travel while undergoing recordings, thus restricting free ambulation in a large-scale environment. Previous studies using EEG/MEG (magnetoencephalogram) and two-dimensionally rendered joystick-based virtual reality (2D VR) suggest that movement-related oscillations tend to manifest specifically within the 1–8 Hz (delta-theta) frequency band (for a review, see Jacobs, 2013). These delta-theta rhythms are typically associated with active, but not passive, navigation in 2D VR (de Araújo et al., 2002); such oscillations can distinguish the presence of landmarks (Sharma et al., 2017) and they can also dissociate landmarks from targets (Weidemann et al., 2009). However, these previous findings on the association between low-frequency oscillations and spatial navigation did not incorporate free ambulation, an important component for movement-related oscillations in the rodent (Chen, King, Burgess, & O'Keefe, 2013; Ravassard et al., 2013). Indeed, one major limitation of 2D desktop VR for better understanding spatial navigation is the absence of body-based locomotion and its accompanying activation of motor, vestibular, proprioceptive systems (Taube, Valerio, & Yoder, 2013).

One available solution to such a limitation is the combination of 3D immersive VR (rendered via a head-mounted display, HMD) and wireless EEG recordings. With the help of an omnidirectional treadmill that maps physical displacement onto those in VR and confines such displacements within the treadmill, 3D immersive VR allows participants to travel infinitely far inside the VR, therefore making it possible to introduce free ambulation while not interrupting scalp EEG recordings. Wireless mobile EEG recording is a novel methodology in which participants actively move about while simultaneously undergoing EEG recordings. Locomotion is generally unconstrained with this methodology, and it has been widely applied in kinematic and gait studies (Castermans, Duvinage, Cheron, & Dutoit, 2014; Snyder, Kline, Huang, & Ferris, 2015; Wagner et al., 2012). As suggested by one study recording scalp EEG of a vertically oscillating mannequin (Oliveira, Schlink, Hairston, König, & Ferris, 2016), noise introduced by this motion can be broadband

and distributed over the scalp. Independent component analysis (ICA, Delorme & Makeig, 2004), however, is effective in improving the signal-to-noise ratio and recovering neural signals even following such artifact-related increases in low-frequency power (Oliveira et al., 2016). In the current study, we are motivated to simulate a more naturalistic experience of spatial navigation using a HMD, omnidirectional treadmill, and a wireless scalp EEG recording system while utilizing ICA to reduce noise contamination.

As a means of assaying our ability to detect bona fide biologically based oscillations under testing conditions potentially involving significant degrees of machine-generated noise, we directly compare our ability to detect the well-characterized 8–12 Hz alpha oscillation, which we expect to manifest under complementary conditions (eyes closed, Berger, 1934) and different recording sites (maximal amplitude over the occipital cortex, Dondey & Klass, 1974). Another value of investigating alpha oscillations is that they are sometimes associated with the upper frequency band (8–12 Hz) of movement-related oscillations in humans (Bohbot et al., 2017), and thus understanding their behavioral correlates, as possibly distinct from FM delta-theta oscillations, is helpful to advancing our knowledge of this important signal. Thus, the aim of the current study is to demonstrate a dissociation between FM delta-theta and occipital alpha oscillations during ambulation and visual stimulation.

Our primary hypothesis, which we term the movement-related FM delta-theta hypothesis, states that FM low-frequency rhythms are associated with locomotion and/or spatial navigation. If FM delta-theta oscillations are movement-related, we expect that they will increase during ambulation compared to standing still, regardless of the presence of visual input during movement. The opposite pattern should hold for alpha oscillations (i.e., they should increase when the eyes are closed, regardless of movement). Furthermore, we predict that FM movement-related delta-theta oscillations and occipital alpha suppression will be topographically selective, with movement-related delta-theta oscillations restricted to the FM region and occipital alpha suppression to the occipital region.

2 | METHOD

2.1 | Participants

Eighteen (9 female) undergraduate students received credit for participating in the study. All participants had normal or corrected-to-normal color vision and normal hearing, weighed 200 lbs or less, and reported no history of cardiovascular problems or motion sickness. Written informed consent was obtained before the experiment, and the methods were approved by the ethical review board at University of California, Davis.
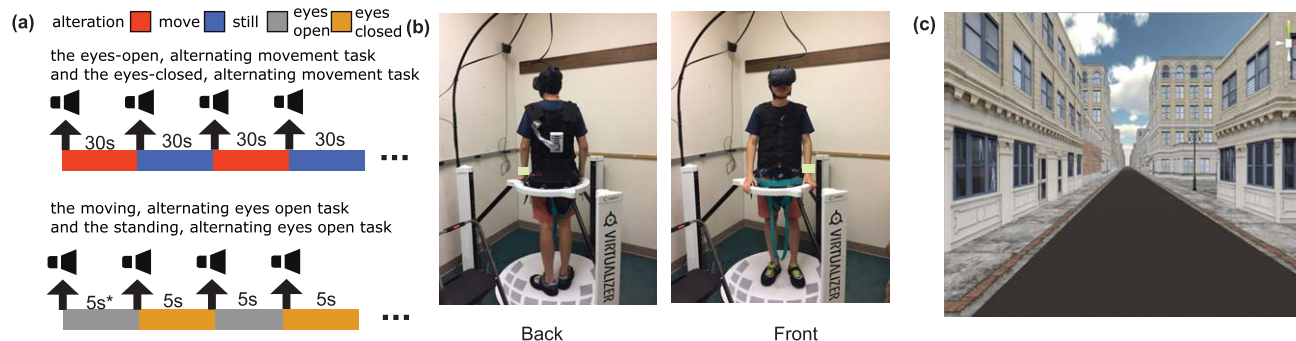
FIGURE 1 Behavioral tasks, testing material, and wireless EEG recording. (a) Participants were asked to complete four tasks sequentially. *Note: for the moving and standing still tasks, the intervals between beeps were 30 s for some participants. (b) Front and back of wireless EEG recording system, coupled with an immersive virtual reality and an omnidirectional treadmill. (c) A snapshot of the virtual environment used in the study

2.2 | Apparatus

EEG was recorded using the wireless ActiCap 64-channel scalp EEG recording system (Brain Products GmbH, Germany), with impedances kept below 25 kΩ. Sampling rate was set to 500 Hz, and the reference site was FCz. Signals were then wirelessly transmitted via the MOVE module (Brain Products).

To simulate the immersive virtual environment, we used HTC Vive HMD and a Cyberith Virtualizer omnidirectional treadmill (Cyberith GmbH, Herzogenburg, Austria). The HTC Vive delivered binocular visual information, and the Cyberith Virtualizer translated the movement in physical space into the locomotion of the avatar in the virtual environment (Figure 1b,c). To program the virtual environment, we used the Unity game engine (version 5.5.0f3).

2.3 | Procedures

All participants first underwent placement of scalp EEG recording electrodes and assays of recording quality by the experimenter. Participants then stood still on the omnidirectional treadmill and watched as the experimenter provided a tutorial for movement on the treadmill, which was intended to minimize vertical movements. Next, they were outfitted with HTC Vive HMD and were immersed in a practice virtual city. In the practice city, participants were asked to explore freely until they reported that they felt confident controlling the motion of the virtual avatar. The practice session was ~5 min.

After the practice, participants were asked to complete four tasks sequentially. In each task, participants heard multiple beep tones at a fixed interval to indicate what they were supposed to do (i.e., move or stand still, open or close eyes). The duration of a beep was 715 ms, and the peak frequency was 1000 Hz. The beeps served as task reminders to avoid extensive reading with the HMD, which could potentially influence oscillations and induce cybersickness. The beep

was played by two stereo speakers. Every time a beep was played, a trigger was sent from the stimulus presentation computer to the EEG amplifier to provide time stamps for behavioral events on the EEG recording computer.

Participants either switched between moving on the treadmill and standing still, or switched between eyes open and eyes shut, according to task demands given by the experimenter before the tasks began. In the first task, they were asked to keep their eyes open throughout the task and, upon hearing beeps, alternated between moving on the treadmill and standing still; we refer to this as the "eyes open, alternating movement" task. In the second task, they were asked to keep their eyes closed and, upon hearing beeps, alternated between moving and standing still; we refer to this as the "eyes closed, alternating movement" task. In the third task, they opened and closed their eyes after each beep, while moving continuously; we refer to this as the "moving, alternating eyes open" task. In the fourth task, the only difference was that participants stood still throughout; we refer to this as the "standing still, alternating eyes open" task (see Figure 1a). Each task lasted ~8 min, and between tasks they rested for 3 min.

In eyes open task and eyes closed task, all participants heard beeps every 30 s, and changed their behavior eight times, constituting eight trials for walking and standing still. In the moving task and standing still task, for five participants, the interstimulus interval (ISI) of beeps was 30s, and they changed their behavior four times, constituting four trials for open and closed eyes. For the rest of the participants, we changed the ISI to 5 s for compliance purposes and to avoid fatigue, and participants in this case changed their behavior 24 times, constituting 24 trials for open and closed eyes.

Although we could not directly observe whether participants were complying with opening or closing their eyes (the eyes were not visible to the experimenter because of the HMD, Figure 1b), we could infer their behavioral states by looking at the EEG raw data. During the tasks, the

PSYCHOPHYSIOLOGY SPR

experimenter paid attention to eyeblink artifacts at electrode sites Fp1 and Fp2, and/or strong and sustained alpha oscillations in occipital electrodes when the eyes of participants should be open, or such oscillations when their eyes should be closed. If the experimenter was concerned, after the data collection for the current task, the experimenter asked participants whether they complied with the task demand. If they did not comply, they were asked to complete the same task again.

Before each task began, participants were instructed on how to minimize movement-related noise in the recordings. When they moved, they were reminded to keep their upper torso stable and to place their hands on the ring of the treadmill if they felt this improved their stability (see Figure 1b). When they navigated in virtual reality, they were instructed to stay on the center of the road and walk at a steady pace. When they opened or closed eyes, they were told to do so gently. They were also asked to hold nonemergency questions and not to speak until the current task was finished.

2.4 | EEG preprocessing

Signals were processed using EEGLAB (Delorme & Makeig, 2004), and were high-pass filtered at 1 Hz. For one of the participants, the signals were rereferenced to Cz, due to the defective reference electrode FCz used for their recording. The kurtosis of each channel was calculated. Channels with kurtosis more than 5 standard deviations away were rejected and interpolated (four and five channels were removed and interpolated for two different subjects, respectively). ICA was then performed on the continuous EEG data. A procedure for semi-automatic selection of independent component (IC) for artifact correction, SAISCA, was used to assist the process of artifact detection (Chaumon, Bishop, & Busch, 2015). For SAISCA, we computed the autocorrelation of the raw signal ("autocorrelation"), focality of IC's topography ("focal"), and focality of IC's amplitude ("focal trial"). Low autocorrelation of an independent component likely indicated muscle artifact, while high spatial or temporal focality likely indicated a bad electrode or rare events (Chaumon et al., 2015). Based on a total of 64 ICs, we first rejected those marked as artifacts by SAISCA at the default threshold (2 standard deviations), and then made decisions for other ICs based on their topographies, power spectra, and temporal activity. Averaged across participants and tasks, we rejected 22.02 independent components out of 64 ($SD = 9.35$; range = 6–40). On average, we removed 15.39 components for eyes open/alternating movement ($SD = 5.54$), 25.17 for eyes closed/alternating movement, ($SD = 10.57$), 24.39 for moving/alternating opening eyes ($SD = 8.40$), and 23.17 for standing still/alternating opening eyes ($SD = 9.38$).

After artifact removal, signals were divided into epochs, with the start of epochs aligned to the start of beeps, and the end of epochs aligned to the start of the next beeps. In the few instances in which the wireless EEG signal was not properly transmitted by the MOVE system and we received blank data, we cropped the trial to minimize the data dropout and maximize the length of continuous signals with satisfactory quality. If the experimenter confirmed visually that no data loss occurred for 30-s epochs, data in the first 3 s and the last 1 s were discarded to avoid edge artifacts; for 5-s epochs, data in the first 1 s and the last 1 s were discarded. The signals were then low-pass filtered at 30 Hz.

2.5 | Spectral analysis and oscillation detection

Power values of specific frequencies in the EEG signals were extracted by convolving the signals with 6-cycle Morlet wavelets (Grossmann, Morlet, & Paul, 1985). We then used the Better OSCillation method (BOSC, Whitten, Hughes, Dickson, & Caplan, 2011) to detect oscillatory activities in the signal. BOSC is designed to detect bouts of oscillatory activity that would otherwise be difficult to detect with spectral decomposition techniques alone. In addition to identifying oscillations in our tasks, BOSC allowed us to better address possible noise confounds that were unrelated to "true" oscillatory signals. For example, because head motions induce spurious delta and theta power increases without the presence of "true" neural activities (Oliveira et al., 2016), BOSC would provide evidence of sustained and oscillatory activities for frequencies of interest, pointing to neural origins for our signals. To be detected by BOSC as an oscillation, the segment of the signal needed to exceed both a power threshold and a duration threshold. Spiking transients and artifacts induced by whole-body movement would therefore not survive the BOSC procedure. The first step was to estimate the background-colored noise spectrum. In the current study, we used the data recorded when participants were standing still with eyes open as the baseline for individual background estimation. The second step was to calculate the amplitude and duration thresholds. We used a 95% confidence level for the power threshold and three cycles as the duration threshold. BOSC then made binary decisions for each time stamp in signals as oscillatory (1) or not (0). $P_{episode}$, a measure for the prevalence of oscillations during an epoch, was defined as the proportion of oscillatory activities within that epoch.

We confined the statistical comparisons to frontal and occipital clusters (see Figure 2), our regions of interest (ROIs), where we expected to see effects of delta-theta and alpha oscillations based on past work cited in the Introduction. For the frontal cluster, we included AFz, AF3, AF4, F3, F1, F2, F4, FC3, FC4, FC1, and FC2. For the occipital cluster, we included Pz, P3, P7, O1, Oz, O2, P4, P8, P1, P5, PO7, PO3, POz, PO4, PO8, P6, P2, and Iz. Then, we
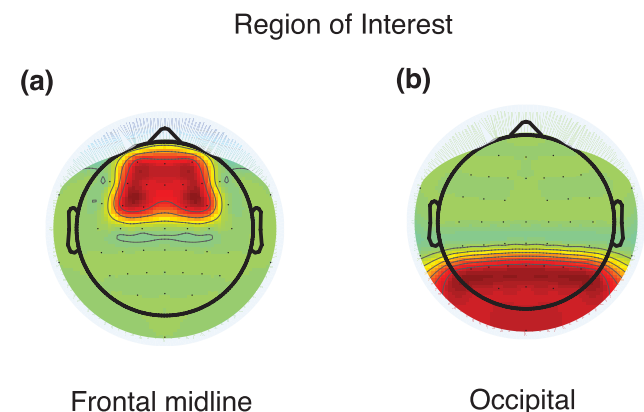
Region of Interest

FIGURE 2 Regions of interest. (a) Frontal-midline cluster. (b) Occipital cluster

collapsed the power estimates and $P_{episode}$ across electrodes within regional clusters.

We investigated frequencies from 2–30 Hz using a log spacing, based on suggestions for better sampling frequencies within the 1/f spectrum (Cohen, 2014). Thus, delta included 2, 2.31, 2.66, 3.07, and 3.54 Hz, theta included 4.08, 4.70, 5.42, 6.26, and 7.21 Hz, alpha included 8.32, 9.59, 11.06, and 12.76 Hz, and beta included 14.71, 16.96, 19.56, 22.56, 26.01, and 30 Hz, which were based on the widely used definitions of these frequency bands in humans (Niedermeyer & Da Silva, 2005). In the current study, we used a functional definition of the theta band (2–8 Hz, Buzsáki, 2005; Jacobs, 2013), grouping together the traditional delta and theta band for analyses. We based this decision on past theoretical proposals and empirical findings suggesting that humans show a broader band of movement-related oscillations than simply within the 4–8 Hz theta band, covering a range from about 1–8 Hz (Bohbot et al., 2017; Jacobs, 2013). We note, however, that restricting our analyses to the delta or theta band alone does not affect our overall finding (see online supporting information, Figure S4, S5, S6, and Table S1.)

We collapsed the power estimates and $P_{episode}$ across trials, participants, and frequencies within bands. After collapsing, $P_{episode}$ values were logit-transformed to correct for nonnormality of paired differences. Logit $P_{episode}$ and power values were compared using repeated measures analyses of variance (ANOVAs), and Greenhouse-Geisser correction

was applied when necessary. For post hoc comparisons of logit $P_{episode}$, we used paired t tests, and for power values, we used Wilcoxon signed-rank tests because of the nonnormality of paired differences. The p values reported are original p values, and we used BKY FDR (Benjamini, Krieger, & Yekutieli, false discovery rate) correction to use more stringent control for multiple comparisons correction (Benjamini, Krieger, & Yekutieli, 2006). After correction, the p threshold for power analyses was .0432, and for $P_{episode}$, .0199.

3 | RESULTS

We first ran 2 ROI $\times$ 2 Frequency Band $\times$ 4 Task $\times$ 2 Alternation four-way ANOVAs on both power values and logit $P_{episode}$ to test whether the effects of Task $\times$ Alternation of changes varied in different combinations of the ROIs and frequency bands. The ROI variable was whether recordings were in the FM or occipital region (see Figure 2). The frequency band variable indicated the range of frequencies (i.e., delta-theta or alpha) of both power and logit $P_{episode}$. The task variable was what participants did throughout the tasks: eyes open, eyes closed, moving, and standing still. The alternation variable was what participants did in an alternative manner while maintaining the continuous behavior. When the task variable was either eyes open or eyes closed, the alternation variable was either moving or standing still; when the task variable was either moving or standing still, the alternation variable was either eyes open or eyes closed.

Both four-way ANOVAs revealed a significant four-way interaction effect (see Table 1 ANOVA; power: $F(3, 51) = 17.12$, *corrected* $p < .0001$, generalized $\eta^2 = .004$, $\varepsilon = .70$; logit $P_{episode}$: $F(3, 51) = 7.90$, *corrected* $p = .001$, generalized $\eta^2 = .003$, $\varepsilon = .71$). Both significant four-way interaction effects indicated that Task $\times$ Alternation had differing effects on the power values and logit $P_{episode}$ depending on Region $\times$ Frequency Band. We used Cohen's d as the indicator of effect sizes (d). See Table 1 and 2 for a summary of ANOVAs and post hoc comparisons. For clarity of presentation, we focus on a specific subset of post hoc tests, as they were designed to test our specific hypotheses. Results from the ANOVAs are reported in Table 1.

TABLE 1 Summary of ANOVA results

	Measures					
	Power			**logit $P_{episode}$**		
ANOVA factors	**Sources**	**F**	**p (uncorrected)**	**Sources**	**F**	**p (uncorrected)**
Frequency-region-task-alternation	Four-way interaction	17.12	< .0001	Four-way interaction	7.90	.0002

Note. If a significant interaction existed, main effects were not included.

TABLE 2 Summary of post hoc comparison p values

Hypothesis	Frequency	Region	Task	Direction of differences	Power	$P_{episode}$
Hypothesis 1 Delta-theta movement-related	Delta-theta	FM	Eyes open	move > still	**< .0001**	**.0008**
			Eyes closed	move > still	**.0007**	.0681
	Alpha	Occipital	Eyes open	move < still	**.0432**	**.0132**
			Eyes closed	move > still	.6705	.1335
Hypothesis 2 Occipital alpha suppression	Alpha	Occipital	Moving	eyes open < closed	**.0056**	**.0059**
			Standing still	eyes open < closed	**.0032**	**.0056**
	Delta-theta	FM	Moving	eyes open > closed	.766	.5423
			Standing still	eyes open < closed	.1187	.3079
Hypothesis 3 Frequency-specificity	Alpha	FM	Eyes open	move < still	.4683	.1607
			Eyes closed	move < still	.154	.3018
	Delta-theta	Occipital	Moving	eyes open < closed	.3692	.3365
			Standing still	eyes open < closed	**.0159**	**.0073**
Hypothesis 4 Topographical specificity	Delta-theta	Occipital	Eyes open	move > still	**.0182**	.2146
			Eyes closed	move > still	**.0304**	.2212
	Alpha	FM	Moving	eyes open < closed	**.0139**	**.0199**
			Standing still	eyes open < closed	**.0269**	.0555

Note. All p values are uncorrected. Using BKY FDR correction, the corrected threshold for power analyses is .0432, and for $P_{episode}$, is .0199. Significant p values appear in bold. FM = frontal-midline.

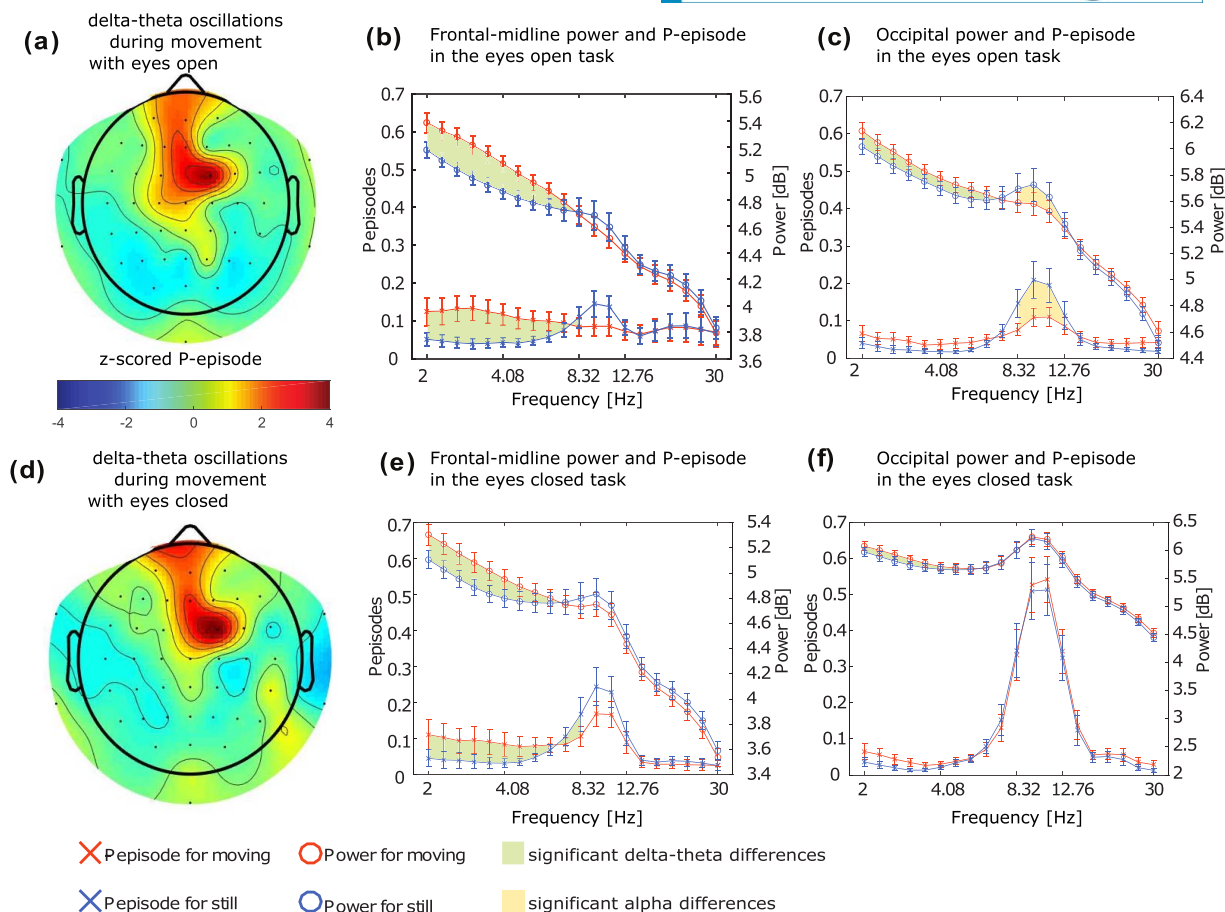## 3.1 | FM delta-theta oscillations are related to movement

Analyses of power values revealed that FM delta-theta oscillations significantly increased during movement regardless of visual input. Post hoc tests revealed that delta-theta power was higher during movement: FM delta-theta band had greater power when participants alternated moving and standing still on the treadmill during the eyes open (see Figure 3b, Wilcoxon signed-rank test, $V = 166$, $p <$ .0001, $M_{movement} = 5.10$, $SD_{movement} = 0.27$; $M_{still} = 4.91$, $SD_{still} = 0.24$) and eyes closed tasks (see Figure 3e, $V = 158$, $p < .001$, $M_{movement} = 5.00$, $SD_{movement} = 0.31$; $M_{still} = 4.87$, $SD_{still} = 0.30$). These findings demonstrate that FM delta-theta increased during movement compared to standing still, regardless of whether eyes were open or shut. These findings support the movement-related FM delta-theta hypothesis in that FM delta-theta oscillations increase with ambulation.

Further, consistent with a specific role for FM delta-theta oscillations in ambulation during navigation, occipital alpha oscillations did not change between movement and standing still periods when participants kept their eyes closed. Post hoc tests revealed that occipital alpha power values did not differ between alternated movement and standing still periods, when eyes were closed (Figure 3f, $V = 96$, $p =$ .67, $M_{movement} = 6.16$, $SD_{movement} = 0.41$; $M_{still} = 6.13$, $SD_{still} = 0.49$). Unexpectedly, we found higher occipital alpha power when participants alternated to standing still compared to movement ($V = 39$, $p = .04$, $M_{movement} = 5.56$,

$SD_{movement} = 0.35$; $M_{still} = 5.68$, $SD_{still} = 0.50$, see Figure 3c) when their eyes were open. These findings suggest that alpha oscillations were not modulated by movement when eyes were closed, but were modulated in the opposite direction as FM movement-related delta-theta oscillations (still > movement) when eyes were open. We return to a more detailed consideration of this finding in the Discussion.

Analyses of $P_{episode}$ showed similar patterns to those of power values reported above (see Figure 4a), and further supported the idea that FM delta-theta, but not occipital alpha oscillations, were associated with movement. Specifically, analyses of $P_{episode}$ values revealed that FM delta-theta oscillations were more prevalent and sustained when participants moved than when they stood still regardless of visual input. Post hoc tests confirmed that FM low-frequency oscillations were more sustained when participants moved compared to when standing still, $t(17) = 4.05$, $p < .001$, 95% CI [0.44, 1.41], $d = 0.89$, *logit*: $M_{movement} = -2.54$, $SD_{movement} = 1.21$; $M_{still} = -3.46$, $SD_{still} = 1.07$; *raw*: $M_{movement} = .12$, $SD_{movement} = 0.12$; $M_{still} = .05$, $SD_{still} = 0.05$, with their eyes open (see Figure 3a,b, 4a), and with their eyes closed, $t(17) = 1.95$, $p = 0.07$, 95% CI [−0.04, 1.09], $d = 0.34$, *logit*: $M_{movement} = -2.94$, $SD_{movement} = 1.27$; $M_{still} = -3.46$, $SD_{still} = 1.08$; *raw*: $M_{movement} = .09$, $SD_{movement} = 0.13$; $M_{still} = .05$, $SD_{still} = 0.07$ (see Figure 3d,e, 4a).

Also, consistent with the results of power changes reported above, post hoc comparisons (see Figure 3f, 4a) showed that occipital alpha $P_{episode}$ did not differ between alternating movement and standing still epochs when eyes

FIGURE 3 FM delta-theta oscillations are movement related regardless of visual input, while occipital alpha oscillations are not movement related. (a) Spatial distribution of z-scored lower-frequency $P_{episode}$ during movement in the eyes open task. (b) Power spectral density and $P_{episode}$ distribution by frequency in frontal-midline ROI in the eyes open task. (c) Power spectral density and $P_{episode}$ distribution by frequency in occipital ROI in the eyes open task. (d) Spatial distribution of z-scored lower-frequency $P_{episode}$ during movement in the eyes closed task. (e) Power spectral density and $P_{episode}$ distribution by frequency in frontal-midline ROI in the eyes closed task. (f) Power spectral density and $P_{episode}$ distribution by frequency in occipital ROI in the eyes closed task

were shut, $t(17) = 1.58$, $p = .13$, 95% CI $[−0.06, 0.38]$, logit: $M_{movement} = −0.26$, $SD_{movement} = 1.49$; $M_{still} = −0.43$, $SD_{still} = 1.74$; raw: $M_{movement} = .47$, $SD_{movement} = 0.28$; $M_{still} = .46$, $SD_{still} = 0.30$, see Figure 3f). However, just as with power, we found alpha oscillations were less prevalent during alternating movement compared to standing still epochs, $t(17) = −2.77$, $p = .01$, 95% CI $[−1.04, −0.14]$, $d = −0.32$, logit: $M_{movement} = −2.73$, $SD_{movement} = 0.35$; $M_{still} = −2.13$, $SD_{still} = 0.50$; raw: $M_{movement} = .10$, $SD_{movement} = 0.09$; $M_{still} = .18$, $SD_{still} = 0.18$ (see Figure 3c) when the eyes were open. Our separate analyses of $P_{episode}$ thus corroborate our findings with power, supporting the movement-related delta-theta hypothesis, but extending it by suggesting that these perturbations in the EEG signals are considered "oscillatory" by BOSC (surviving a minimum of three cycles) rather than simple transient events in the EEG pattern.

Interestingly, besides confirming the movement-related delta-theta hypothesis, we noticed that FM delta-theta prevalence during the movement > still comparison increased when visual input was present (i.e., participants kept their

eyes open). We conducted a paired t test to test whether the differences in FM delta-theta logit $P_{episode}$ were larger during movement > still in the eyes open task compared to the eyes closed task. Indeed, when participants kept their eyes open, the scale of movement-induced FM delta-theta oscillations was marginally higher compared to when participants kept their eyes closed, $t(17) = 1.91$, $p = .07$, 95% CI $[−0.04, 0.84]$, $d = 0.26$, $M_{diff.open} = 0.93$, $SD_{diff.open} = 0.97$; $M_{diff.closed} = 0.52$, $SD_{diff.closed} = 1.14$. These findings suggest that visual input via optic flow, in addition to body-based cues, may serve as an additional driver of movement-related FM delta-theta oscillations (Warren, Kay, Zosh, Duchon, & Sahuc, 2001).

3.2 | Occipital alpha oscillations are suppressed by opening eyes

To ensure that our movement-related oscillatory findings were not somehow an artifact of noise related to our recordings, despite our best efforts to mitigate these using ICA, we

also investigated alpha oscillations, which should be modulated by primarily visual stimulation and not by movement when alternating eyes open and eyes shut. Indeed, post hoc comparisons revealed that occipital alpha had higher power during the movement task when alternating between eyes open and eyes shut ($V = 24$, $p < .01$, $M_{open} = 5.78$, $SD_{open} = 0.41$; $M_{closed} = 6.19$, $SD_{closed} = 0.49$, see Figure 5b) and the standing still task ($V = 25$, $p < .01$, $M_{open} = 5.76$, $SD_{open} = 0.43$; $M_{closed} = 6.23$, $SD_{closed} = 0.56$, see Figure 5e). In contrast, FM delta-theta power, as predicted, did not differ significantly as a result of alternating opening and shutting eyes in the moving ($V = 78$, $p = .77$, see Figure 5c) and standing still tasks ($V = 49$, $p = .12$, see Figure 5f).

Analyses of $P_{episode}$ provided similar conclusions that occipital alpha suppression (see Figure 4b; i.e., a greater prevalence of alpha oscillations during eyes closed than eyes open alternation regardless of movement). Specifically, alpha was higher during the moving task when the eyes were closed: $t(17) = 3.14$, $p < .01$, 95% CI $[-2.55, -0.50]$, $d = -0.68$, logit: $M_{open} = -1.91$, $SD_{open} = 1.21$; $M_{closed} = -0.38$, $SD_{closed} = 1.67$; raw: $M_{open} = .17$, $SD_{open} = 0.13$; $M_{closed} = .45$, $SD_{closed} = 0.28$ (see Figure 5a,b) and standing still task: $t(17) = 3.17$, $p < .01$, 95% CI $[-2.48, -0.50]$, $d = -0.76$, logit: $M_{open} = -1.70$, $SD_{open} = 1.16$; $M_{closed} = -0.22$, $SD_{closed} = 1.75$; raw: $M_{open} = .20$, $SD_{open} = 0.15$; $M_{closed} = .50$, $SD_{closed} = 0.31$ (see Figure 5d,e). In contrast, FM delta-theta prevalence did not differ between alternations of eyes open versus closed either in the moving task, $t(17) = -0.62$, $p = .54$, 95% CI $[-0.29, 0.16]$, logit: $M_{open} = -2.06$, $SD_{open} = 1.43$; $M_{closed} = -1.99$, $SD_{closed} = 1.15$; raw: $M_{open} = .18$, $SD_{open} = 0.18$; $M_{closed} = .17$, $SD_{closed} = 0.14$ (see Figure 5c) nor the standing still task, $t(17) = -1.05$, $p = .31$, 95% CI $[-0.58, 0.20]$, logit:

$M_{open} = -3.93$, $SD_{open} = 0.41$; $M_{closed} = -3.74$, $SD_{closed} = 0.79$; raw: $M_{open} = .02$, $SD_{open} = 0.01$; $M_{closed} = .03$, $SD_{closed} = 0.02$ (see Figure 5f). Thus, we confirmed that visual stimulation suppressed alpha oscillations during alternation of eyes open and eyes shut, suggesting that our recordings did not significantly impair our ability to detect an otherwise prominent oscillatory signal like alpha.

3.3 | FM movement-related delta-theta increases and occipital alpha suppression are frequency specific

An important corollary of the movement-related FM delta-theta hypothesis is that such oscillations should increase specifically within the delta-theta but not alpha bands and that occipital alpha suppression by vision is specific to the alpha, but not delta-theta bands. To address this issue, we first compared FM alpha power changes in the eyes open and eyes closed tasks during alternation of movement. If the FM movement-related delta-theta oscillations were frequency specific, we would expect to see few FM movement-related alpha oscillations. Post hoc tests showed that FM alpha power did not change during movement compared to standing still epochs in the eyes open ($V = 68$, $p = .47$, $M_{movement} = 4.60$, $SD_{movement} = 0.30$; $M_{still} = 4.66$, $SD_{still} = 0.45$, see Figure 3b) and eyes closed tasks ($V = 52$, $p = .15$, $M_{movement} = 4.72$, $SD_{movement} = 0.37$; $M_{still} = 4.79$, $SD_{still} = 0.50$, see Figure 3e). Analyses of $P_{episode}$ further corroborated the frequency-specificity of FM movement-related delta-theta oscillations (see Figure 4c) movement compared to standing still during eyes open task: $t(17) = -1.47$, $p = .16$, 95% CI $[-1.23, 0.22]$, logit: $M_{movement} = -3.04$, $SD_{movement} = 1.37$; $M_{still} = -2.54$, $SD_{still} = 1.65$; raw:
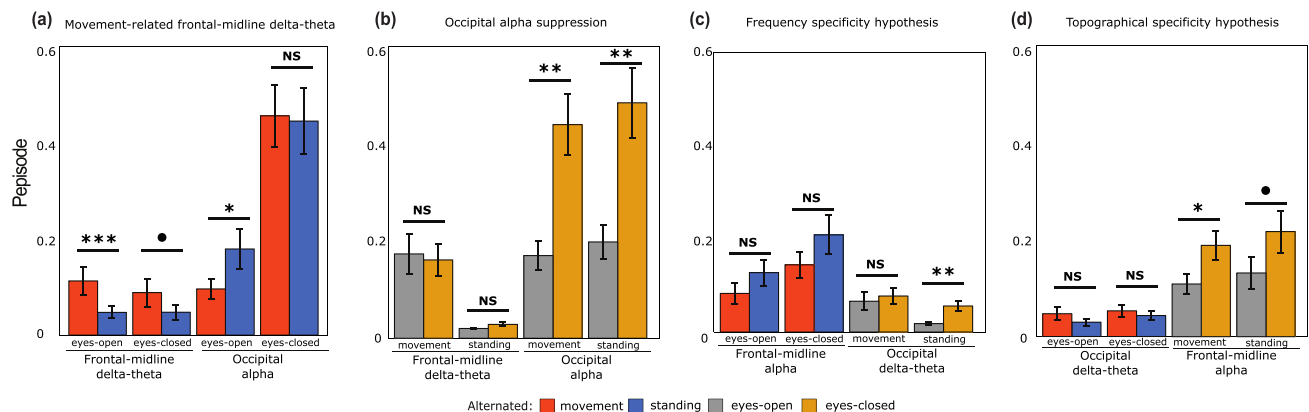

FIGURE 4 Double dissociation of FM movement-related delta-theta and occipital visually suppressed alpha oscillations. (a) FM delta-theta oscillations increased during movement, regardless of visual input, while occipital alpha was not responsive to movement. (b) Occipital alpha oscillations were suppressed by opening eyes, while FM delta-theta oscillations did not change. (c) When FM movement-related delta-theta oscillations were induced, FM alpha oscillations did not increase. When the occipital alpha suppression was induced, occipital delta-theta oscillations did not change with movement. These findings confirmed the frequency-specificity hypothesis. (d) When FM movement-related delta-theta oscillations were induced, occipital delta-theta oscillations did not increase. When the occipital alpha suppression was induced, FM alpha oscillations were also suppressed, but to a lesser magnitude compared to (b) and (d). •$p < .10$; *$p < .0199$; **$p < .01$; ***$p < .001$

$M_{movement} = .09$, $SD_{still} = 0.10$; $M_{movement} = .13$, $SD_{still} = 0.12$ (see Figure 3b) and eyes closed task, $t(17) = -1.06$, $p = .30$, 95% CI $[-0.61, 0.20]$, *logit*: $M_{movement} = -2.09$, $SD_{movement} = 1.11$; $M_{still} = -1.89$, $SD_{still} = 1.66$; *raw*: $M_{movement} = .15$, $SD_{movement} = 0.12$; $M_{still} = .21$, $SD_{still} = 0.18$ (see Figure 3e). These findings again show that FM movement-related increases were specific to delta-theta but not alpha bands. In contrast, post hoc tests again showed that occipital delta-theta power did not differ during eyes open epochs compared to eyes closed epochs during the moving task ($V = 64$, $p = .37$, $M_{open} = 5.89$, $SD_{open} = 0.29$; $M_{closed} = 5.92$, $SD_{closed} = 0.31$, see Figure 5b), although occipital delta-theta had higher power during eyes closed epochs compared to eyes open epochs in the standing still task ($V = 31$, $p = .02$, $M_{open} = 5.71$, $SD_{open} = 0.26$; $M_{closed} = 5.85$, $SD_{closed} = 0.33$, see Figure 5e).

$P_{episode}$ analyses of occipital delta-theta oscillations provided for similar results, showing that occipital delta-theta prevalence was not different during eyes open epochs

compared to eyes closed epochs in the movement task, $t(17) = -0.99$, $p = .34$, 95% CI $[-0.68, 0.24]$, *logit*: $M_{open} = -3.44$, $SD_{open} = 1.52$; $M_{closed} = -3.22$, $SD_{closed} = 1.68$; *raw*: $M_{open} = .07$, $SD_{open} = 0.08$; $M_{closed} = .08$, $SD_{closed} = 0.08$ (see Figure 5b), although occipital delta-theta oscillations were again more prevalent when eyes were closed compared to when eyes were open in the standing still task, $t(17) = 3.05$, $p = .01$, 95% CI $[-1.47, -0.27]$, $d = -0.59$, *logit*: $M_{open} = -4.15$, $SD_{open} = 0.60$; $M_{closed} = -3.29$, $SD_{closed} = 1.18$; *raw*: $M_{open} = .02$, $SD_{open} = 0.01$; $M_{closed} = .06$, $SD_{closed} = 0.05$ (see Figure 5e). The findings, based on power and $P_{episode}$ taken together, support the frequency-specificity of occipital alpha suppression by vision: occipital delta-theta oscillations, unlike occipital alpha oscillations, were not affected overall by opening and closing eyes, although they did show a tendency toward greater prevalence during eyes closed compared to the eyes open epochs when standing still. In this way, we confirmed the frequency-specificity of occipital alpha to eyes closed
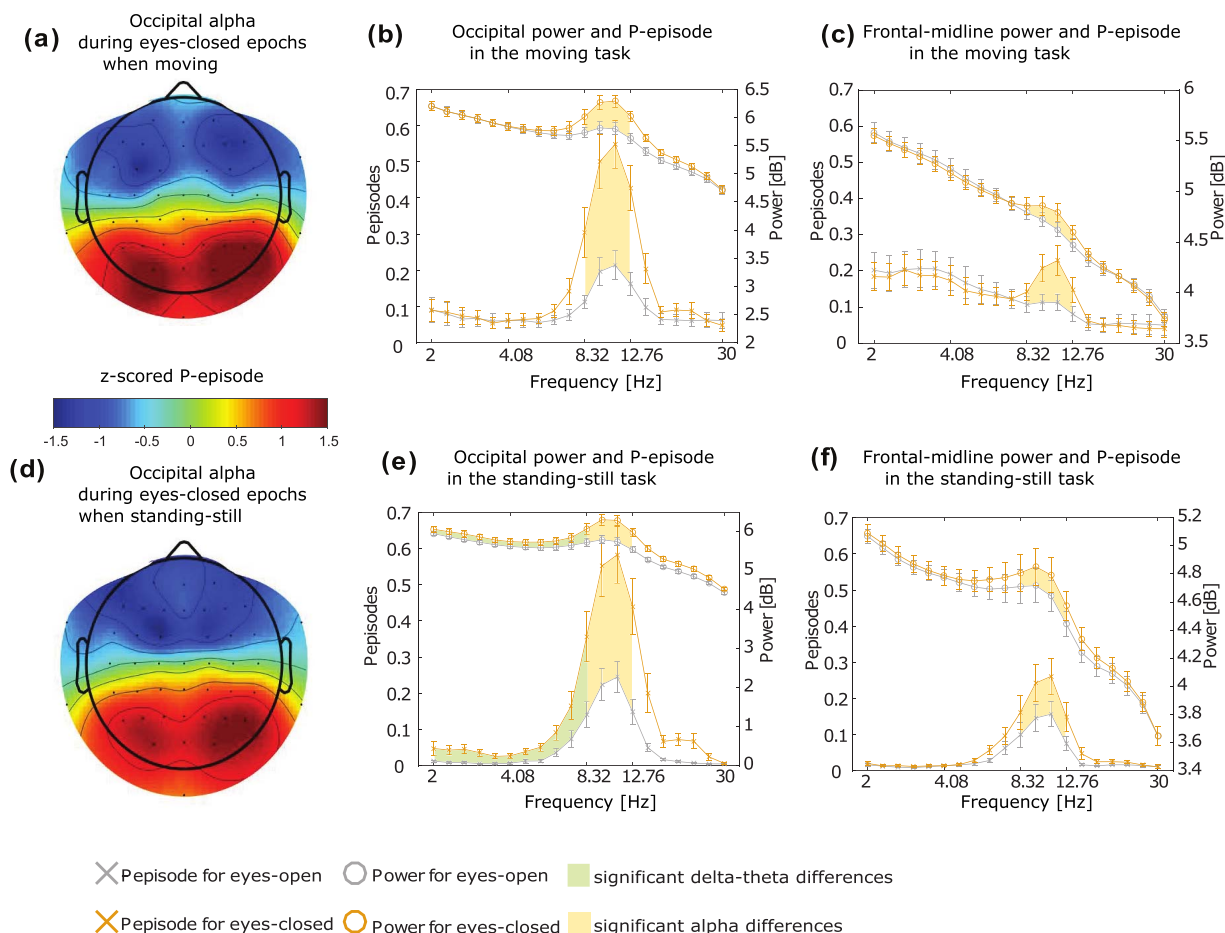
FIGURE 5 Occipital alpha oscillations are suppressed by visual stimulation while FM delta-theta oscillations are not. (a) Spatial distribution of *z*-scored alpha $P_{episode}$ during eyes closed epochs in the moving task. (b) Power spectral density and $P_{episode}$ distribution by frequency in occipital ROI in the moving task. (c) Power spectral density and $P_{episode}$ distribution by frequency in frontal-midline ROI in the moving task. (d) Spatial distribution of *z*-scored alpha $P_{episode}$ during eyes closed epochs in the standing still task. (e) Power spectral density and $P_{episode}$ distribution by frequency in occipital ROI in the standing still task. (f) Power spectral density and $P_{episode}$ distribution by frequency in frontal-midline ROI in the standing still task

versus eyes open more generally, with the caveat that occipital delta-theta showed decreases when the eyes were open during standing still.

3.4 | Movement-related delta-theta increases are topographically specific

To address whether FM delta-theta movement-related oscillations were topographically specific, we also wished to test whether movement-related delta-theta oscillations were specific to the frontal-midline region, and whether alpha suppression by vision was primarily limited to the occipital recording sites. Overall, our analyses supported the idea that FM movement-related delta-theta oscillations did not extend to the occipital region (see Figure 4d). Although occipital delta-theta power was higher during movement compared to standing still in the eyes open task ($V = 139$, $p = .02$, $M_{movement} = 5.83$, $SD_{movement} = 0.24$; $M_{still} = 5.76$, $SD_{still} = 0.25$, see Figure 3c) and the eyes closed task ($V = 135$, $p = .03$, $M_{movement} = 5.82$, $SD_{movement} = 0.34$; $M_{still} = 5.76$, $SD_{still} = 0.36$, see Figure 3f), this was not true for $P_{episode}$. Specifically, occipital delta-theta prevalence was not different during movement epochs compared to standing still epochs in the eyes open task, $t(17) = 1.29$, $p = .21$, 95% CI [-0.19, 0.77], $logit$: $M_{movement} = -3.67$, $SD_{movement} = 1.36$; $M_{still} = -3.96$, $SD_{still} = 1.12$; raw: $M_{movement} = .05$, $SD_{movement} = 0.06$; $M_{still} = .03$, $SD_{still} = 0.03$ (see Figure 3a,c) and eyes closed task, $t(17) = 1.27$, $p = .22$, 95% CI [-0.19, 0.77], $logit$: $M_{movement} = -3.61$, $SD_{movement} = 1.61$; $M_{still} = -3.90$, $SD_{still} = 1.73$; raw: $M_{movement} = .05$, $SD_{movement} = 0.05$; $M_{still} = 0.04$, $SD_{still} = .04$ (see Figure 3d,f). Given the oscillatory nature of the BOSC method we used to compute $P_{episode}$, we believe that the movement-related occipital delta-theta power increases were likely caused by transients, but not oscillations, and therefore we conclude that FM movement-related delta-theta oscillations were topographically specific and restricted to the FM region (Figure 4c).

Our next set of analyses looked at the topographical specificity of occipital alpha suppression by vision. The results, however, argued against the topographical specificity of occipital alpha suppression, and they showed that, in the frontal-midline region, similar oscillatory changes manifested as in the occipital region. Post hoc comparisons revealed that FM alpha power was higher during eyes closed epochs compared to eyes open epochs in the moving task ($V = 30$, $p = .01$, $M_{open} = 4.71$, $SD_{open} = 0.29$; $M_{closed} = 4.84$, $SD_{closed} = 0.37$, see Figure 5c) and the standing still task ($V = 35$, $p = .03$, $M_{open} = 4.69$, $SD_{open} = 0.48$; $M_{closed} = 4.82$, $SD_{closed} = 0.53$, see Figure 5f). A closer look at the suppression induced by vision at FM recording sites showed that the FM alpha suppression was smaller in scale compared to the occipital alpha suppression. In other words,

the differences for alpha power between eyes open and eyes closed were smaller at the FM than at occipital regions, regardless of whether participants moved, $t(17) = 2.27$, $p = .04$, 95% CI [0.02, 0.55], $d = 0.54$, $M_{diff.FM} = 0.12$, $SD_{diff.FM} = 0.21$; $M_{diff.occ} = 0.41$, $SD_{diff.occ} = 0.50$, or stood still, $t(17) = 2.35$, $p = .03$, 95% CI [0.04, 0.65], $d = 0.55$, $M_{diff.FM} = 0.12$, $SD_{diff.FM} = 0.21$; $M_{diff.occ} = 0.47$, $SD_{diff.occ} = 0.58$.

Analyses of $P_{episode}$ also demonstrated the same pattern: FM alpha oscillations were more prevalent and sustained during eyes closed epochs compared to eyes open epochs in the moving, $t(17) = 2.57$, $p = .02$, 95% CI [0.12, 1.20], $d = 0.41$, $logit$: $M_{open} = -2.40$, $SD_{open} = 1.00$; $M_{closed} = -1.75$, $SD_{closed} = 1.14$; raw: $M_{open} = .11$, $SD_{open} = 0.09$; $M_{closed} = .19$, $SD_{closed} = 0.13$ (see Figure 5c) and the standing still task, $t(17) = 2.06$, $p = .06$, 95% CI [-0.01, 1.07], $d = 0.29$, $logit$: $M_{open} = -2.31$, $SD_{open} = 1.28$; $M_{closed} = -1.79$, $SD_{closed} = 1.56$; raw: $M_{open} = .13$, $SD_{open} = 0.14$; $M_{closed} = .22$, $SD_{closed} = 0.19$ (see Figure 4d, 5f). Such FM alpha prevalence changes were also smaller in scale compared to those of the occipital alpha prevalence, both when participants moved, $t(17) = -2.70$, $p = .02$, 95% CI [0.04, 0.34], $d = 0.64$, $M_{diff.FM} = 0.09$, $SD_{diff.FM} = 0.12$; $M_{diff.occ} = 0.28$, $SD_{diff.occ} = 0.31$, and when they stood still, $t(17) = -2.64$, $p = .02$, 95% CI [0.04, 0.38], $d = 0.62$, $M_{diff.FM} = 0.09$, $SD_{diff.FM} = 0.12$; $M_{diff.occ} = 0.29$, $SD_{diff.occ} = 0.34$. These findings taken together suggested that alpha suppression induced by visual stimulation was present, to some extent, at FM recording sites, although to a lesser extent than the occipital region.

4 | DISCUSSION

The principal finding of this study is that low-frequency delta-theta oscillations at the frontal-midline region have higher power and are more sustained during physical movement than when standing still on an omnidirectional treadmill coupled with 3D immersive virtual reality. Such movement-related delta-theta oscillations are also more pronounced when visual input from the spatial environment is present. Furthermore, we showed a double dissociation between FM delta-theta movement-related increases and occipital alpha suppression, suggesting their behavioral independence. Our findings suggest that frontal-midline low-frequency oscillations can be induced by movement, via a combination of visual, vestibular, and proprioceptive information.

We first compared the power and prevalence of FM delta-theta and occipital alpha during movement versus standing still epochs. We found that, during movement, FM delta-theta oscillations had higher power and were more sustained during free ambulation when compared to standing still, regardless of the presence of visual input. Furthermore,

FM delta-theta oscillations were more prevalent when visual information was present compared to when absent. In contrast, occipital alpha oscillations did not respond to movement when the eyes were closed, and were suppressed by movement when the eyes were open. In contrast, FM delta-theta did not respond to the suppression of visual input, regardless of whether participants were moving or standing still. To rule out the possibility that what we observed as FM delta-theta movement-related increases were simply systematic recording noises caused by movement, we tested whether the increases of FM delta-theta oscillations were frequency selective (i.e., extended to FM alpha), and whether the increases of FM delta-theta oscillations were topographically selective (i.e., extended to occipital delta-theta). We confirmed that FM movement-related delta-theta did not extend to the alpha band or occipital region. This was also confirmed by the strong presence of occipital alpha suppression, which occurred during both movement and standing still. If oscillatory signals were merely a result of noise induced by movement on the treadmill, or noise from the head-mounted display due to head movements, we would not expect to record selective increases in well-characterized alpha oscillations during visual suppression. Thus, such findings also suggest that we overcame significant noise artifacts during ambulation with visual input to record biological oscillations with scalp EEG.

Surprisingly, the behavior of occipital alpha deviated from our previous hypotheses of being uninfluenced by movement. We found some evidence that occipital alpha oscillations were suppressed by movement with visual input, opposite to the pattern we observed for FM delta-theta. The size of the movement-induced occipital alpha suppression, though, was small compared to the suppression from eyes opening. Furthermore, occipital alpha decreased during movement only in the very first task (see Figure 4a, $P_{episode}$ of alpha in the occipital recording sites in the eyes open task). One possible explanation is that occipital alpha, considered as the representation of cortical idling (Pfurtscheller, Stancák, & Neuper, 1996), indexed the degree of physical relaxation. Movement on the treadmill in the very first task might be difficult for participants and less cognitively demanding as other tasks rolled on. Another plausible explanation is that such occipital alpha increases were volume conduction of somatomotor mu rhythms, an issue we consider in more detail shortly and explore in the supporting information (see Figure S1, S2). While future experiments would be needed to dissociate mu and alpha in more detail in our paradigm, the unexpected movement suppression of occipital alpha does not confound our interpretation of a double dissociation because it was in the opposite direction (still > movement) to FM delta-theta.

We also found that alpha oscillations were suppressed by vision in the FM region, arguing somewhat against the topographical specificity of alpha in our tasks. However, we do not think this rendered the occipital alpha suppression global or artifactual. It is possible that alpha, as a particularly powerful and robust signal recorded with scalp EEG, may manifest more widely than at occipital cortex (Caplan et al., 2003; Nunez, Wingeier, & Silberstein, 2001). It could also be that FM alpha signals instead reflected resting-related mu oscillations (Pfurtscheller et al., 1996). However, if the FM alpha oscillations were in fact mu oscillations, we might not have expected to see increases in such mu oscillations when participants closed versus opened their eyes, given that mu rhythm over the sensorimotor cortex has been reported to manifest during resting versus movement periods (Pfurtscheller et al., 1996). Thus, in this way, while the FM alpha oscillations we reported have some similarities with mu oscillations, they also differed in other ways and as such cannot be considered bona fide mu oscillations.

Taken together, the current study confirms that spatial navigation and ambulation are potential drivers of frontal-midline low-frequency oscillations in healthy human participants, with the salience of FM delta-theta during both visual input and ambulation compared to the other tasks in our study providing an indirect link to its role in navigation. FM theta has been documented to be correlated with solving arithmetic tasks (Arellano & Schwab, 1950), working memory maintenance, and episodic encoding and retrieval (Hsieh & Ranganath, 2014), and sensorimotor integration (Cruikshank, Singhal, Hueppelsheuser, & Caplan, 2012). Active spatial navigation requires processing of incoming sensory stimuli and producing correct motor output, also known as sensorimotor integration (Bland & Oddie, 2001). Although our past results argue against a sensorimotor explanation for hippocampal delta-theta oscillations (Vass et al., 2016), our findings cannot address this issue for FM delta-theta oscillations. Active spatial navigation also requires the acquisition of landmarks and routes of the environment explored, which inevitably involves the cognitive processes of working memory maintenance, item encoding, and retrieval (Kahana, 2006). Therefore, it is not surprising that FM theta oscillations are involved during movement.

From the perspective of coherence between FM scalp theta and hippocampal theta oscillations, it is also not surprising that we found an association between FM delta-theta oscillations and movement. Hippocampal low-frequency oscillations increase proportionately with running speed in rats (Czurko, 1999), are modulated by locomotion and spatial navigations, and locomotion-related theta increases are accompanied by increased corticohippocampal coherence (Young & McNaughton, 2009). This evidence suggests that FM delta-theta recorded with scalp EEG and hippocampal low-frequency oscillations recorded with invasive EEG may potentially share some functional similarities. In this study,

we did not localize the sources generating the movement-related delta-theta oscillations, but our results indirectly indicate that human midline cortex theta-band activities might also be driven by the same cognitive processes as those for hippocampal theta oscillations. We believe that our study is the first to demonstrate FM movement-related delta-theta oscillations in a large-scale virtual environment with free ambulation and therefore greater ecological validity than desktop VR (Taube et al., 2013).

Given that FM delta-theta oscillations are movement-related, an important question regarding the functional role of FM delta-theta oscillations arises. Are they contributing to those cognitive processes unique to spatial navigation, for example, transformation between egocentric and allocentric representations (Gramann et al., 2010)? Further studies can investigate what behavioral and cognitive components in the context of treadmill movement coupled with VR modulate FM delta-theta increases, such as speed, task, or spatial view (Watrous et al., 2011). We also speculate that FM delta-theta oscillations can be a potential carrier of spatial information during navigation, like distance from the start point or distance to goal (Bush et al., 2017; Vass et al., 2016). Additionally, it is intriguing that we observed increases in both delta and theta oscillations during free ambulation and spatial navigation, inconsistent with previous findings in rats that midline cortical theta activities increase during locomotion coupled with decreases in delta band power in midline cortex (Green & Arduini, 1954). Our results of movement-related delta oscillations increases do not align with midline cortical delta decreases during locomotion in rats, and this will need to be addressed in future studies.

Overall, our study provides novel evidence for a double dissociation between FM delta-theta and occipital alpha oscillations. In our current study, we believe that this double dissociation shows the modularity and separability of movement-related low-frequency activities, imposing stronger constraints on theoretical models. In contrast, we did not aim at demonstrating the exact number of cognitive processes underlying FM theta and occipital alpha, which is the most frequent purpose of double dissociations (Baddeley, 2003). Rather, our study provides a strong rationale that the FM delta-theta oscillations we recorded arise from biological rather than noise-based signals and are evoked by distinct aspects of our tasks. Our study thus provides a means of investigating recording quality during ambulation with a HMD on a treadmill, both of which produce significant electrical noise contamination, by employing occipital alpha oscillations as a potential control comparison. Our findings also expand our understanding of the behavioral correlates of frontal-midline low-frequency oscillations, and the neural correlates of spatial navigation involving vestibular input.

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SUPPORTING INFORMATION

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Figure S1
Figure S2
Figure S3
Figure S4
Figure S5
Table S1