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Research Report

Dissociation of motor control from motor awareness in awake sleepwalkers: An EEG study in virtual reality

Yannick Rothacher [a,1], *Anh Nguyen* [b,1], *Evdokia Efthymiou* [a,1], *Esther Werth* [a,c], *Christian R. Baumann* [a,c], *Bigna Lenggenhager* [c,d], *Peter Brugger* [e,f], *Andreas Kunz* [b] *and Lukas L. Imbach* [a,c,g,*]

[a] *Department of Neurology, University Hospital and University of Zurich, Zurich, Switzerland*
[b] *Innovation Center Virtual Reality, ETH Zurich, Zurich, Switzerland*
[c] *Sleep & Health Zurich, University of Zurich, Zurich, Switzerland*
[d] *Department of Psychology, Cognitive Neuropsychology, University of Zurich, Zurich, Switzerland*
[e] *University Hospital of Psychiatry PUK, Zurich, Switzerland*
[f] *Rehabilitation Center Valens, Valens, Switzerland*
[g] *Swiss Epilepsy Clinic, Klinik Lengg, Zurich, Switzerland*

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ABSTRACT

Recent behavioral evidence from a virtual reality (VR) study indicates that awake sleepwalkers show dissociation of motor control and motor awareness. This dissociation resembles the nocturnal disintegration of motor awareness and movement during episodes of sleepwalking. Here, we set out to examine the neural underpinnings of altered motor awareness in sleepwalkers by measuring EEG modulation during redirected walking in VR. To this end, we measured scalp EEG during ongoing motor behavior to provide information on motor processing and its modulation in VR. Using this approach, we discovered distinct EEG patterns associated to dual tasking and sub-threshold motor control in sleepwalkers compared to control subjects. These observations provide further electrophysiological evidence for the proposed brain-body dissociation in awake sleepwalkers.

This study shows proof-of-principle that EEG biomarkers of movement in a VR setting add to the understanding of altered motor awareness in sleepwalkers. In a broader perspective, we confirm the feasibility of using the additional dimensionality in VR providing novel diagnostic biomarkers not accessible to conventional clinical investigations. In future studies, this approach could contribute to the diagnostic work-up of patients with a broad spectrum of neurological diseases.

* *Corresponding author*. Swiss Epilepsy Clinic, Klinik Lengg, Zurich, Switzerland.
E-mail address: lukas.imbach@kliniklengg.ch (L.L. Imbach).

[1] Equal contribution.

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1. Introduction

Patients suffering from parasomnia can enter a nocturnal dissociative state of body wakefulness and mind sleep (Bassetti et al., 2000). Complex behaviors, including walking ('sleepwalking') or speaking, are executed in the absence of overt consciousness, while the brain remains in deep sleep (Arnulf, 2018). Being aware of one's motor actions is a key aspect of the individual's bodily self (Castiello et al., 1991; David et al., 2008; Weiss et al., 2014). In sleepwalkers, this mutual interaction between volitional control and bodily movements is temporarily decoupled during episodes of parasomnia. Sleepwalking can thus be conceptualized not only as an arousal disorder, but also as a *disorder of motor awareness in sleep*. Importantly, this dysfunctional brain state emerges exclusively during deep sleep, while awake sleepwalkers show normal performance in neurological or cognitive assessments. Therefore, diagnosis of parasomnia typically requires sleep examinations in specialized clinics. However, in a recent inspiring study, Kannape and co-workers (Kannape et al., 2017) used a virtual reality (VR) paradigm to unmask altered motor awareness in sleepwalkers: Implementing a walking paradigm with deviated feedback, the authors investigated sleepwalkers while modulating motor control and perception. The core finding of the study was that sleepwalkers maintained more stable motor control and better motor awareness while walking under cognitive load, indicating a multi-tasking advantage. These findings imply that awake sleepwalkers might utilize different brain networks for unaware motor control also during wakefulness.

We set out to test this hypothesis by measuring EEG activity in a VR paradigm analogous to the one used by Kannape et al. (2017) to measure on-line electrophysiological biomarkers of motor control. To this end, we analyzed central beta EEG power, a measure known to be reduced prior to and during actual and imagined motor behavior (Imbach et al., 2015; Klopp et al., 2001; Kühn et al., 2004; Schaller et al., 2017). Conversely, *higher* beta power in precentral cortical areas has been connected to lower cognitive load and more intrinsic (unaware) motor control (Bichsel et al., 2018). In a similar vein, we recently found *high* beta activity in an invasive electrophysiological study during episodes of REM sleep parasomnia (Hackius et al., 2016). This fueled our hypothesis that beta power might be differentially modulated in awake sleepwalkers performing a motor task as compared to controls. Considering the superior motor performance under cognitive load for sleepwalkers in Kannape's study, we expected higher beta activity (corresponding to automated or unaware motor control) in awake sleepwalkers, especially under dual task conditions.

2. Methods

2.1. *Experimental design*

We recruited 15 patients (f: 7 and m: 8, mean age 30.6 y, range 22–47) with confirmed diagnosis of NREM parasomnia based on previous state-of-the-art sleep laboratory examinations (video-polysomnography) and 15 age and gender matched control subjects (Table 1) and measured the (leftward) redirection threshold in a single and dual-task (serial-7 subtraction) paradigm in both groups. Simultaneously, a non-invasive scalp EEG using the international 10/20 montage (23 surface electrodes) was recorded. EEG activity was measured for 20 min at rest (prior to entering the VR environment) and during the entire experiment. We used a mobile EEG device to measure EEG during motor tasks (Trex HD amplifier, Natus Neuroworks) with a standard EEG cap (GVB Multicap). EEG was sampled at 512 Hz.

For the redirection threshold estimation, participants wore an Oculus DK2 HMD and were connected to an Intersense IS-1200 optical tracking system for 6 DOF head position tracking at 180 Hz (Foxlin & Naimark, 2003) (Fig. 1). In redirected walking the virtual environment (VE) is rotated around the user, forcing him/her onto a curved pathway and consequently causing a mismatch between the visually perceived and the physically performed walking trajectory (Rothacher et al., 2018). The experimental setup is depicted in Fig. 1, showing a participant in VR under variable feedback distortion that allowed for determining the subjective redirection threshold similar as in Kannape et al. In contrast to Kannape's work, we implemented a first-person VR-perspective and a longer walking trajectory (Appendix and Table 1). Based on the subjective motor awareness, we distinguished motor behavior as either *sub-threshold* (not aware of redirection) or *supra-threshold* (aware of redirection, Fig. 1). This paradigm is an extension of the classical paradigm for measuring hand agency by Fournet and Jeannerod (Fourneret & Jeannerod, 1998). Thus, to increase the generalizability of our approach, we also determined redirection thresholds in an upper limb task. To this end, participants controlled a cursor on the digitizer tablet from a starting to a target position. Similar to the feedback distortion used in redirected walking, a redirection was induced into the movements of the cursor and all movements were classified as either sub- or supra-threshold as defined above. EEG activity was also measured during the upper limb task (for details on the experimental procedures see Appendix).

2.2. *EEG post-processing*

To quantify the modulation of spectral EEG properties during the motor tasks, we first calculated the average power spectral density (PSD) during both tasks using a modified periodogram (Welch, 1967) approach (256 samples Hanning window, 50% window overlap, 512 Hz sampling rate). Raw spectral power during movement was calculated in a common reference montage for grand average spectra (Fig. 2A and B). In a next step, to account for individual baseline differences as compared to resting state, we normalized the raw EEG data to baseline values for each frequency band, resulting in higher relative beta power in sleepwalkers compared to controls (Fig. 2C). Finally, the beta band EEG power was mapped according to location of the scalp electrodes. Relative beta power in a bipolar montage from the region showing the most prominent modulation (C4-Cz, Fig. 2D) was then used for all further linear model analyses (Fig. 3). Cz was used a local reference to the C4 electrode in a bipolar montage to suppress myogenic (movement) artifacts. No electrode clustering was

Table 1 – Comparison of behavioral effects in Kannape et al. (2017) and the current study including velocity, redirection threshold, accuracy for the implemented walking and drawing paradigms. Analyzed variables are shown in column 4, tested interactions between variables are marked with a colon between variables (e.g. task:group). *p* values from a linear mixed model analysis for the dependent variable (column 1) are given in column 5.

	Kannape et al.	Current study	Variable	*p*-value
Subjects	11 sleepwalkers, 11 controls	15 sleepwalkers, 15 controls		
	matched gender and age, 7 male	matched gender only, 7 male		
	age: 26 ± 13 years old	sleepwalker: 31 ± 8.5 years old		
		controls: 26 ± 4 years old		
	handedness not mentioned	one left handed subject in each group		
Experiment design	projection screen	head mounted display		
	third person perspective	first person perspective		
	walking distance = 1.8 m	walking distance = 7.5 m		
	yes/no threshold identification	two-alternative forced choice task		
	redirection both left and right	only redirecting to the left		
Walking velocity	controls slowed down in dual task	decrease in both groups in dual task	task	<.005
	sleepwalker maintained similar velocity in dual task			
	no gender effect	no gender effect	velocity	n.s.
Walking threshold	no difference in single task	no difference in either group in single task	group	n.s.
	increase in control in dual task	increase in both groups in dual task	task	<.05
	decrease in sleepwalkers in dual task		task	<.005
	significant interaction between task	no significant interaction	type:task	n.s.
	not reported	higher threshold for female	gender	<.0005
Walking accuracy (deviation from path)	no significant difference across tasks	no difference across tasks	task	n.s.
	not reported	no gender effect	gender	n.s.
Drawing velocity	–	interaction between task condition and group	task:group	n.s.
Drawing threshold	–	no difference in either group in single task	group	n.s.
	–	increase in both groups in dual task	task	<.05
	–	no significant interaction between task condition and subject type	type:task	n.s.
	–	gender effect: higher threshold for female	gender	<.0005
Drawing accuracy	–	no difference across task condition, subject type and other factors	group	n.s.
			task	n.s.
			gender	<.05
			age	n.s.
			order	n.s.
			task:group	n.s.
Correlation between drawing and walking threshold	–	significant bivariate correlation		<.005

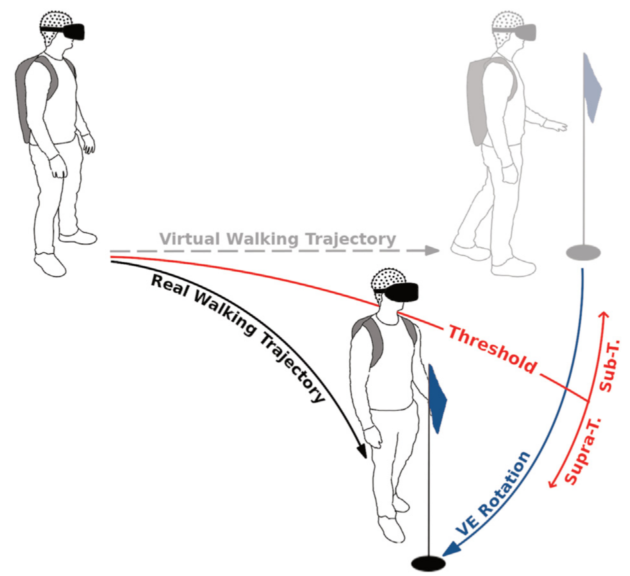

Fig. 1 – Experimental setup. Illustration of a walking trajectory manipulation through redirected walking with simultaneous measurement of surface EEG. Alternative forced choice was used to determine the individual redirection threshold. For trajectories below the threshold, participants are unaware of redirection (sub-threshold), while they are aware of redirection above (supra-threshold). Note that while the depiction shows an example of rightward redirection to facilitate visualization, in the experiment redirection was applied to the left side.

performed for statistical analysis. We implemented a spectral-based artifact rejection (excluding epochs with gamma power (>30 Hz) 3 times over the individual median. The number of rejected trials due to artifacts was not different between the groups (8% for sleepwalkers *vs* 9% for controls).

2.3. *Statistical analysis*

We used R (R Core Team, 2017) to perform a linear mixed model analysis for the relationship between beta power (dependent variable) and group (sleepwalker/controls), task (dual/single) and redirection awareness (subthreshold/suprathreshold/control condition) as independent variables, respectively. Separate mixed models were calculated to analyze the interaction between the group with task and redirection awareness (Fig. 3A and B). Individuals were included as random variables. We controlled for age, gender and handedness and circadian effects (morning *vs* afternoon measurement). All *p*-values were obtained by likelihood ratio tests. For post-hoc comparisons (data in Fig. 3), we applied the Satterthwaite method with Tukey adjustment. All analyses were repeated in the same way with the exclusion of the two left handed participants, showing the same significant effects as reported. For comparison of EEG power between sleepwalkers and controls in different EEG bands (Fig. 2C), we applied a 2-way ANOVA using frequency band and group as dependent variables and performed post-hoc group comparisons to identify the bandwidth in which the two groups differ significantly.

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

3. Results

Our analysis focused on (i) reproducing the findings of Kanape et al. on a behavioral level and (ii) investigating the modulation of central EEG beta power during the experimental procedures.

3.1. *Behavioral findings*

We analyzed multiple behavioral markers for motor behavior and motor awareness during redirected walking as summarized in Table 1. As in the preceding study (Kannape et al., 2017), walking accuracy and velocity were not significantly different between the two groups (Table 1). Also in agreement with Kannape et al., the subjective redirection threshold showed no difference between the groups in the single task condition. However, under cognitive load (dual tasking), we found a significant reduction of walking velocity for both groups, whereas Kannape et al. reported stable walking velocity for sleepwalkers (Kannape et al., 2017). Furthermore and also in contrast to Kannape et al., we found no significant interaction between the study groups and conditions (single *vs* dual task) for the redirection threshold. Whereas Kannape et al. found a decreased redirection threshold selectively in the sleepwalker group, our paradigm showed increased redirection threshold in both groups in the dual task condition (Table 1). We have performed a sensitivity analysis to get an estimate of the minimum effect size of an interaction between group and task that could have reliably yielded a statistically significant result given our sample size. Using a simulation-based approach with a significance level of 5% and 10′000 repetitions for each effect size, the sensitivity analysis indicated that an interaction of size .058 could have been detected with a power of more than 80%, which is an effect size slightly larger than the observed main effect of the dual task (increase in redirection thresholds by .036). The results found in the upper limb paradigm were analogous to the walking task. The analysis of the drawing task revealed an increased redirection threshold in both groups in the dual task condition without interaction between task and groups (Table 1, bottom). The redirection thresholds of the walking and drawing tasks were positively correlated (see Table 1). Therefore, participants who showed high sensitivity to redirection when walking, were also more perceptive of redirection in the drawing task.

3.2. *EEG modulation during redirected walking*

We first calculated the average EEG power while moving in both groups to determine the spectral region of interest. This analysis showed a consistent increase of spectral power for sleepwalkers relative to the control group in the theta, low alpha and beta bands (Fig. 2A and B). To adjust for inter-individual variability of the raw EEG amplitude and background beta power, we normalized the beta power during

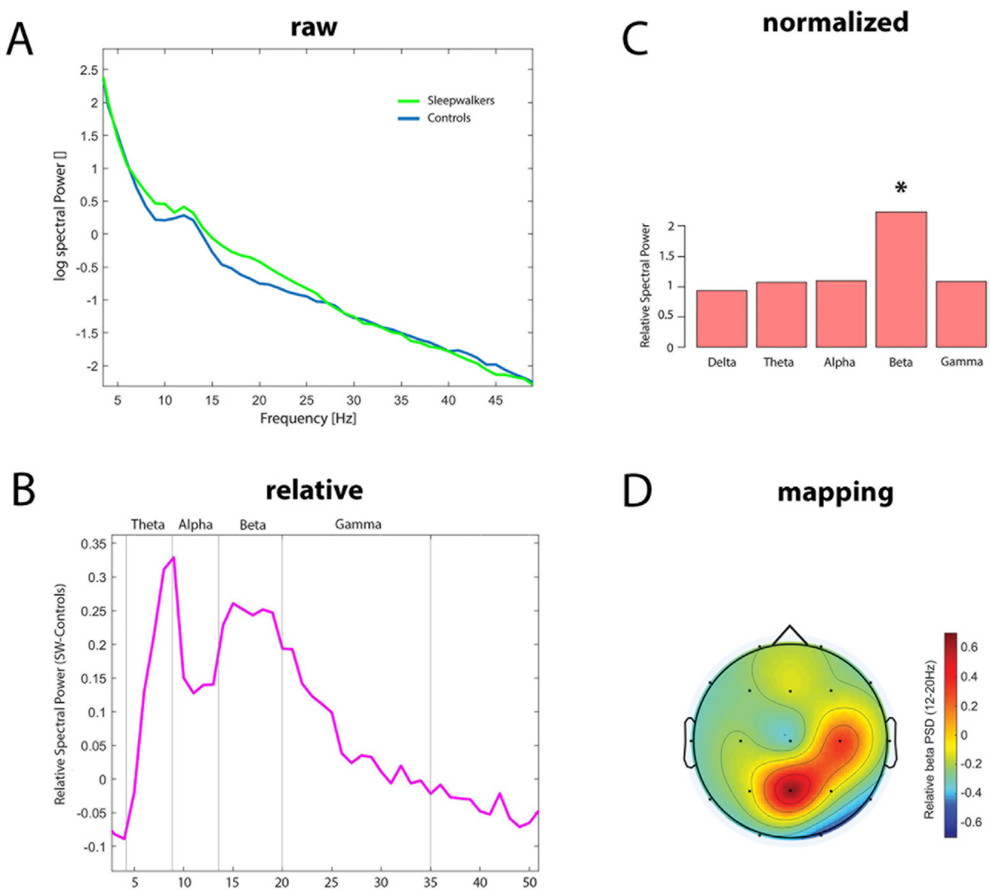

Fig. 2 – Spectral Analysis. (A) Absolute and (B) relative spectral power raw data (Sleepwalkers − Controls) as average of all trials only during walking (redirected and non-redirected) for both groups. Positive values in panel B indicate higher average power in sleepwalker as compared to controls. (C) Group means (sleepwalker *vs* controls) for different power bands as indicated in panel B after normalization to pre-movement baseline for each frequency band (resting state). **$p < .05$* in two-way ANOVA (band x group) post-hoc analysis. Mean values are normalized to the control average, values above 1 indicate higher spectral power in sleepwalkers. (D) Mapping of normalized beta EEG power (13–20 Hz) during walking in sleepwalkers (percentage sleepwalkers relative to control subjects in log scale). Positive values indicate higher beta power for sleepwalkers (significant differences in C3, C4 and Pz). Electrode positions according to the 10/20 system are shown as black dots (with linear interpolation on a Cartesian grid). Delta: .5–4 Hz, Theta: 4–8 Hz, Alpha: 8–12 Hz, Beta: 12–20 Hz, Gamma: 20–50 Hz.

movement to the average beta power in the resting condition prior to movement initiation (baseline, Fig. 2C). This normalization also accounts for possible vigilance effects (e.g. increased diffuse beta or temporal theta activity due to daytime sleepiness) across groups. After this step, the relative increase in spectral power during movement for sleepwalkers versus controls showed a more pronounced and highly specific pattern with only the beta power band showing an increased activity (Fig. 2C). Two-way ANOVA post-hoc group comparisons revealed a significant group difference in power only for the beta bandwidth ($p < .05$). To define the cortical region with the most prominent increase in beta power, we finally performed an EEG mapping analysis based on all recorded electrodes. Here we found a consistent beta elevation in sleepwalkers as compared to controls, most prominently over the central electrodes (C3/C4, Fig. 2D). Nonparametric permutation test, accounting for multiple comparisons (Winkler et al., 2016) revealed significant changes for electrodes C3, C4 and Pz. We then used normalized central beta power (C4-Cz, 12–20 Hz) for further group comparisons and modelling of interactions.

The bivariate comparison between the groups showed overall higher relative beta power in sleepwalkers over the right central region in the lower beta band (Fig. 2B and C). We focused therefore on the interaction of relative central beta activity with the experimental conditions (dual *vs* single tasks) and subjective awareness of redirection. Here, we found higher relative beta power in sleepwalkers under cognitive load, whereas in the single task condition no significant group effect was observed (Fig. 3B).

We finally analyzed beta power in relation to the subjective redirection threshold during unbiased walking (no redirection), subthreshold redirected walking (unaware of redirection) and supra-threshold redirection (aware of redirection) to account for the interaction of motor control with individual motor awareness. This analysis revealed significantly higher

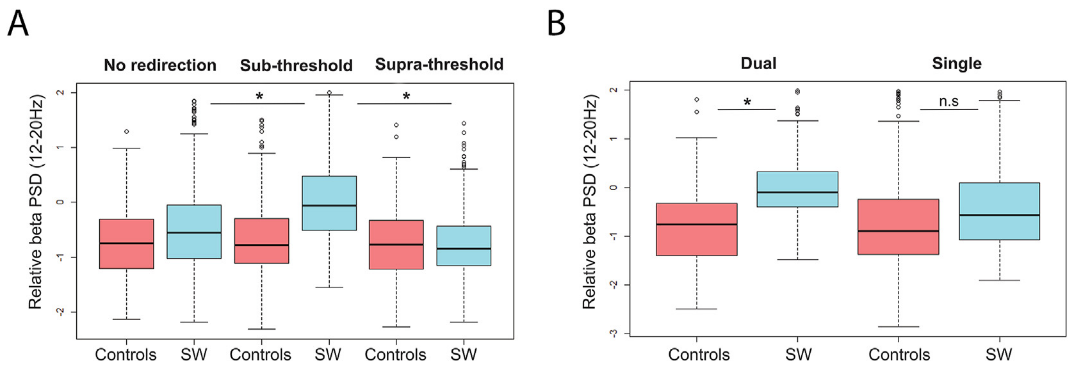

Fig. 3 – (A) Beta power relative to baseline (resting condition) during redirected walking is higher for sleepwalkers (SW) in the sub-threshold condition (middle panel, significant interaction between group and condition $p < .005$). Post-hoc comparison showed significant differences for sleepwalkers in sub-threshold as compared to both other conditions (*$p < .005$), but not for controls (n.s.). (B) Beta power relative to baseline (resting condition) is higher in sleepwalkers under dual task condition (significant interaction, *$p < .05$) Post-hoc comparison shows a significant difference between sleepwalkers and controls only in dual task condition (*$p < .05$). Beta PSD was normalized to pre-experimental resting condition (set to zero).

beta power in subthreshold redirected walking in sleepwalkers, but no difference in control subjects (Fig. 3A). In other words, sleepwalkers shift towards higher beta power while being unaware of the redirection. In the analysis of the drawing task, we observed analogous, yet less pronounced results (Supplementary Figure 1). As in the walking paradigm, drawing thresholds showed also no significant difference between groups on a behavioral level (Table 1). The central EEG showed the same pattern of higher beta power in subthreshold condition that was also present in the upper-limb task (Supplementary Figure 1A). The group effects under cognitive load were however not observed to the same extent during the drawing task (Supplementary Figure 1B).

4. Discussion

While using a VR paradigm of redirected walking similar to Kannape's study (Kannape et al., 2017), we failed to reproduce their main behavioral finding of a reduced redirection walking threshold under cognitive load in sleepwalkers. This disagreement might be due to the first-person perspective implemented in our study, allowing for a more effective redirection in both groups. Alternatively, the use of a head-mounted display in our study may have facilitated redirection over using a back-projection screen as in Kannape's study (Kannape et al., 2017). However, as other behavioral findings (e.g. effects on walking velocity, single task walking threshold) were reproduced in our study, we argue that our VR paradigm provides a valid representation of redirection and motor awareness. Nevertheless, as the number of participants was small in both studies, a smaller effect size in our paradigm due to the head-mounted display might explain the negative behavioral result. Ultimately, a comparative study exploring the behavioral effects in both experimental setups would be the only option to clarify this issue.

However, the novelty we provide here is the electrophysiological correlate for the dissociation of motor execution and motor awareness in awake sleepwalkers. Despite the negative behavioral findings, we observed significant differences in EEG beta power between the groups. In particular, we found that the EEG patterns observed in sleepwalkers showed higher relative beta power under cognitive load and in subthreshold redirected walking (Fig. 3). Central alpha/beta band EEG activity in humans is primarily observed at rest (known as mu-rhythm) and demonstrates event-related-desynchronization prior to voluntary movements with sustained suppression during movement execution. Importantly, the amount of beta-desynchronization depends on the type of motor action. For instance, studies in Parkinson's patients showed that intrinsically paced automated movements leave cortical beta power at baseline level, whereas externally cued goal-directed motor control leads to stronger beta desynchronization (Bichsel et al., 2018). In line with this, in a previous invasive study in sleepwalkers, we also found *higher* beta activity during unaware nocturnal movements in REM sleep parasomnia. These studies thus indicate that higher beta power might correspond to more automated (unaware) motor behavior. Here, we also observe a bias towards higher beta power in awake sleepwalkers selectively under cognitive load, a state corresponding to unaware movement automation. This particular modulation of EEG control in sleepwalkers echoes the previous behavioral observation of improved movement automation under cognitive load in Kannape et al. We argue that our findings complement these observations by documenting the sleepwalkers' dissociation not only on a behavioral level, but also based on altered EEG biomarkers of motor control. As the same effects were also observed in an analogous task for the upper-limb (Supplementary Figure 1), these findings can be interpreted as a characteristic higher-level property of altered motor control in sleepwalkers. The observed EEG changes in our study might thus provide insights in the neural underpinning for the altered motor control in sleepwalkers as observed by Kannape et al. In this way, both studies (albeit using different VR paradigms and technologies) showed evidence for dissociation between motor execution and motor control in sleepwalkers, but in different modalities. Nevertheless, further studies are needed for a direct comparison of the different VR-paradigms on a behavioral and electrophysiological level.

In conclusion, our findings offer an intriguing electrophysiological explanation for the recurrent nocturnal episodes with unconscious motor action through dual task control while simultaneously remaining in deep sleep. Finally, we provide further evidence that selective manipulation of motor control using a virtual environment can reveal significant differences in awake sleepwalkers as compared to control subjects, and might add to their diagnostic evaluation.

Author contributions

Conceptualization, LLI, PB, AK, EW; Methodology, LLI PB AK BL.; Investigation, EE, AN, YR; Writing –Original Draft, LLI.; Writing –Review & Editing, all authors; Resources,CB, EW.; Supervision, LI, PB and AK.

Open practices

The study in this article earned an Open Materials badge for transparent practices. The EEG datasets generated during and/or analysed during the current study are not publicly available, but are available for anonymized review from the corresponding author on request (considering review of data quality, spectral data and/or reproducibility of performed analyses).

Declaration of competing interest

The authors declare no competing interests.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2021.12.016.

Appendix 1. Participants and Procedures

Participants

All patients had a history of nocturnal episodes including sleepwalking. Eight patients had a positive family history for NREM parasomnia. Eight patients also reported injuries from nocturnal episodes. Based on the Edinburgh Handedness Inventory (Oldfield, 1971), 11 patients were right-handed, two patients were ambidextrous and 2 were left-handed. To avoid chronobiological effects on behavior and EEG, we randomly measured half of the patients (7 patients) in the morning hours (08.30) and the remaining half at noon (12:30).

For our control group, we included 15 age and gender matched healthy volunteers (f: 8 and m: 7) without sleep-related disorders. To match for handedness, we included two left-handed and 13 right-handed participants. The control group has a mean age of 26 y (range 22–39, not significantly different as compared to the patients).

All participants signed an informed consent prior to starting the experiment. All experimental procedures were approved by the Cantonal Ethics Committee of Zurich (BASEC number: 2019–00195) and carried out in accordance with the ethical standards of the Declaration of Helsinki. The conditions of ethics approval do not permit public archiving of anonymized study data. Readers seeking access to the data should contact the corresponding author (LLI) or the local ethics committee of Zurich (*Kantonale Ethikkommission Zurich*), Access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data. Specifically, requestors must meet the following conditions to obtain the data (completion of an ethical approval and formal data sharing agreement). No part of the study procedures or analyses was pre-registered prior to the research being conducted.

Detailed experimental procedure

For each participant, the redirection threshold was assessed under a control condition and a dual-task condition. In the control condition, participants started at one end of a 12 m × 6 m tracking area and found themselves in an empty virtual room with a red pillar 7.5 m in front of them. Redirection thresholds were determined in a two-alternative forced choice task (2AFC task). Participants were asked to walk straight to the red pillar for two consecutive trials. In only one of the two trials, a leftward redirection of a specific intensity was applied. To familiarize the participants with the virtual environment and the different paradigms, we performed six trial runs (3 with and without redirection) for both the single and the dual tasks condition. Training runs were balanced between groups to ensure the same level of habituation. For the VR paradigm a custom code was written (publicly available at: https://osf.io/p6akc/?view_only=b03de39ee7c746faa23cab6fccdce070). Only one-sided redirection was applied to increase power and reliability of the subsequent EEG analysis. After completion of the two trials, participants were asked in which of the two trials the redirection had taken place. Depending on the correctness of the answer, the tested redirection intensity was adapted in the next round. In total, each participant completed 50 rounds in each condition. The selection of the tested intensities and the final estimation of the detection threshold was done using the Bayesian-based adaptive threshold estimation procedure QUEST (Watson & Pelli, 1983). QUEST uses a psychometric function to model the probability of giving a correct answer for a specific redirection. The psychometric function starts at a guessing rate of 50% for low redirection gains and approaches a perfect detection rate for strong redirection gains. The detection threshold is classically determined as the stimulus intensity correctly detected in 75% of the cases. The individual detection threshold was determined for each participant and compared between groups. Furthermore, we used the individual redirection threshold for classification of each trial in subthreshold and supra-threshold walking. Trials with redirection without subjective awareness were labelled as subthreshold, whereas suprathreshold redirection refers to trial with subjective redirection awareness. This classification was then used to compare EEG biomarkers between walking trials with and without awareness of redirection (Fig. 3). In total, in each group 1450 trials were performed (725 trials for the control condition and 725 trials for the dual-task condition). Of the 1450 trials with redirection, 595 were in subthreshold and 855 in supra-threshold condition with no significant difference between groups.

In the dual-task condition, the threshold estimation followed the same general procedure. However, participants were requested to perform a serial-7 subtraction task while walking towards the virtual target. Specifically, before starting each trial, participants were shown a randomly generated two-digit number on the screen. Starting with this number, participants had to continuously subtract the number seven (while walking) and report the solutions verbally. The starting values of the serial-7 subtraction task were set between 70 and 100 to make sure that no negative numbers were reached in a trial.

Each condition took approximately 30 min. The order of the two conditions was randomized and counterbalanced over participants. Before starting the redirection threshold estimation, participants performed a short series of training trials in both conditions in order to get used to the redirection procedure.

For the modulation of motor awareness and motor control for an upper limb task, we implemented a similar VR task as follows: Participants sat upright in front of a tablet (WACOM digitizer tablet PTH 651, 370 × 275 mm) wearing an HMD (Oculus DK2). In the HMD, participants were presented with a rectangular field, representing the drawing board from a bird's eye perspective. Participants controlled a cursor on this field using a stylus on the digitizer tablet. For each trial, a starting and target position were indicated on the field. After moving the stylus to the starting position, the task for participants was to guide the pen straight to the target position on the other side of the rectangular field. Similar to the feedback distortion used in redirected walking, a redirection was induced into the movements of the cursor. Participants had to perform a curved drawing motion to counteract this manipulation and to guide the cursor straight to the target. The estimation of the detection thresholds of the induced feedback distortion was performed in the same fashion as for redirected walking (2AFC task). Because of the shorter amount of time needed for drawing compared to walking, more trials were performed. In total, 2320 trials were performed in each group (1160 trials for the control condition and 1160 trials for the dual-task condition). The dual task consisted of the same serial-7 subtraction task used in the redirected walking threshold estimation. To prevent participants from performing very quick drawing motions, a timer (visually represented as a clock) signalized participants the time in which they were supposed to reach the target position. Trials with a slower or faster drawing speed were labeled as invalid trials and were repeated.

REFERENCES

Arnulf, I. (2018). *Seminars in Cancer Biology, 28*, R1288–R1289.

Bassetti, C., Vella, S., Donati, F., Wielepp, P., & Weder, B. (2000). SPECT during sleepwalking. *Lancet, 356*, 484–485.

Bichsel, O., Gassert, R., Stieglitz, L., Uhl, M., Baumann-Vogel, H., Waldvogel, D., Baumann, C. R., & Imbach, L. L. (2018). Functionally separated networks for self-paced and externally-cued motor execution in Parkinson's disease: Evidence from deep brain recordings in humans. *Neuroimage, 177*, 20–29.

Castiello, U., Paulignan, Y., & Jeannerod, M. (1991). Temporal dissociation of motor responses and subjective awareness. A study in normal subjects. *Brain, 114*(Pt 6), 2639–2655.

David, N., Newen, A., & Vogeley, K. (2008). The "sense of agency" and its underlying cognitive and neural mechanisms. *Consciousness and Cognition, 17*, 523–534.

Fourneret, P., & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia, 36*, 1133–1140.

Foxlin, E., & Naimark, L. (2003). VIS-tracker: A wearable vision-inertial self-tracker. In *IEEE virtual reality, 2003. Proceedings* (pp. 199–206).

Hackius, M., Werth, E., Sürücü, O., Baumann, C. R., & Imbach, L. L. (2016). Electrophysiological evidence for alternative motor networks in REM sleep behavior disorder. *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience, 36*, 11795–11800.

Imbach, L. L., Baumann-Vogel, H., Baumann, C. R., Sürücü, O., Hermsdörfer, J., & Sarnthein, J. (2015). Adaptive grip force is modulated by subthalamic beta activity in Parkinson's disease patients. *Neuroimage Clin, 9*, 450–457.

Kannape, O. A., Perrig, S., Rossetti, A. O., & Blanke, O. (2017). Distinct locomotor control and awareness in awake sleepwalkers. *Current Biology: CB, 27*, R1102–R1104.

Klopp, J., Marinkovic, K., Clarke, J., Chauvel, P., Nenov, V., & Halgren, E. (2001). Timing and localization of movement-related spectral changes in the human peri-rolandic cortex: Intracranial recordings. *Neuroimage, 14*, 391–405.

Kühn, A. A., Williams, D., Kupsch, A., Limousin, P., Hariz, M., Schneider, G.-H., Yarrow, K., & Brown, P. (2004). Event-related beta desynchronization in human subthalamic nucleus correlates with motor performance. *Brain, 127*, 735–746.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113.

R Core Team. (2017). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rothacher, Y., Nguyen, A., Lenggenhager, B., Kunz, A., & Brugger, P. (2018). Visual capture of gait during redirected walking. *Scientific Reports, 8*. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6299278/. (Accessed 26 June 2020).

Schaller, F., Weiss, S., & Müller, H. M. (2017). EEG beta-power changes reflect motor involvement in abstract action language processing. *Brain and Language, 168*, 95–105.

Watson, A. B., & Pelli, D. G. (1983). Quest: A bayesian adaptive psychometric method. *Perception & Psychophysics, 33*, 113–120.

Weiss, C., Tsakiris, M., Haggard, P., & Schütz-Bosbach, S. (2014). Agency in the sensorimotor system and its relation to explicit action awareness. *Neuropsychologia, 52*, 82–92.

Welch, P. (1967). The use of fast fourier transform for the estimation of power spectra: A method based on time averaging over short, modified periodograms. *IEEE Transactions on Audio and Electroacoustics, 15*, 70–73.

Winkler, A. M., Webster, M. A., Brooks, J. C., Tracey, I., Smith, S. M., & Nichols, T. E. (2016). Nonparametric combination and related permutation tests for neuroimaging. *HumBrain Mapp, 37*, 1486–1511. https://doi.org/10.1002/hbm.23115