How natural walking changes occipital alpha oscillations and concurrently modulates cognitive processes

Die Auswirkungen natürlichen Gehens auf okzipitale Alpha-Oszillationen bei gleichzeitiger Modulation kognitiver Prozesse

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List of publications

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2) **Chen, X**., Cao, L., & Haendel, B. F. (2022). Differential effects of walking across visual cortical processing stages. Cortex, 149, 16-28.
3) **Chen, X**., Cao, L., & Haendel, B. F. (2022). Human visual processing during walking: Dissociable pre-and post-stimulus influences. NeuroImage, 264, 119757.

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Parts of this thesis contain the following unpublished manuscripts:

4) **Chen, X**., Cao, L., Wieske, R.E., Gramann, K., & Händel, B. (in prepration). Walking modulates active auditory sensing.
5) Händel, B. F., **Chen, X**., & Murali, S. (under review). Reduced occipital alpha power marks a movement induced state change that facilitates creative thinking. *shared first authorship

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A detailed statement of individual author contributions can be found in Appendix C and D.

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Summary

Humans actively interact with the world through a wide range of body movements. To understand human cognition in its natural state, we need to incorporate ecologically relevant body movement into our account. One fundamental body movement during daily life is natural walking. Despite its ubiquity, the impact of natural walking on brain activity and cognition has remained a realm underexplored.

In electrophysiology, previous studies have shown a robust reduction of ongoing alpha power in the parieto-occipital cortex during body movements. However, what causes the reduction of ongoing alpha, namely whether this is due to body movement or prevalent sensory input changes, was unknown. To clarify this, study 1 was performed to test if the alpha reduction is dependent on visual input. I compared the resting state alpha power during natural walking and standing, in both light and darkness. The results showed that natural walking led to decreased alpha activity over the occipital cortex compared to standing, regardless of the lighting condition. This suggests that the movement-induced modulation of occipital alpha activity is not driven by visual input changes during walking. I argue that the observed alpha power reduction reflects a change in the state of the subject based on disinhibition induced by walking. Accordingly, natural walking might enhance visual processing and other cognitive processes that involve occipital cortical activity.

I first tested this hypothesis in vision. Study 2 was performed to examine the possible effects of natural walking across visual processing stages by assessing various neural markers during different movement states. The findings revealed an amplified early visual response, while a later visual response remain unaffected. A follow-up study 3 replicated the walking-induced enhancement of the early visual evoked potential and showed that the enhancement was dependent on specific stimulus-related parameters (eccentricity, laterality, distractor presence). Importantly, the results provided evidence that the enhanced early visual responses are indeed linked to the modulation of ongoing occipital alpha power. Walking also modulated the stimulus-induced alpha power. Specifically, it showed that when the target appeared in the fovea area without a distractor, walking exhibited a significantly reduced modulation of alpha power, and showed the largest difference to standing condition. This

effect of eccentricity indicates that during later visual processing stages, the visual input in the fovea area is less processed than in peripheral areas while walking.

The two visual studies showed that walking leads to an enhancement in temporally early visual processes which can be predicted by the walking-induced change in ongoing alpha oscillation likely marking disinhibition. However, while walking affects neural markers of early sensory processes, it does not necessarily lead to a change in the behavioural outcome of a sensory task. The two visual studies suggested that the behavioural outcome seems to be mainly based on later processing stages.

To test the effects of walking outside the visual domain, I turned to audition in study 4. I investigated the influence of walking in a particular path vs. simply stepping on auditory processing. Specifically, the study tested whether enhanced processing due to natural walking can be found in primary auditory brain activity and whether the processing preferences are dependent on the walking path. In addition, I tested whether the changed spatial processing that was reported in previous visual studies can be seen in the auditory domain. The results showed enhanced sensory processing due to walking in the auditory domain, which was again linked to the modulation of occipital alpha oscillation. The auditory processing was further dependent on the walking path. Additionally, enhanced peripheral sensory processing, as found in vision, was also present in audition.

The findings outside vision supported the idea of natural walking affecting cognition in a rather general way. Therefore in my study 5, I examined the effect of natural walking on higher cognitive processing, namely divergent thinking, and its correlation with the modulation of ongoing alpha oscillation. I analyzed alpha oscillations and behavioural performance during restricted and unrestricted movement conditions while subjects completed a Guilford's alternate uses test. The results showed that natural walking, as well as missing body restriction, reduces the occipital alpha ongoing power independent of the task phase which goes along with higher test scores. The occipital alpha power reduction can therefore be an indicator of a changed state that allows improved higher cognitive processes.

In summary, the research presented in this thesis highlights that natural walking can change different processes in the visual and auditory domain as well as higher cognitive

processes. The effect can be attributed to the movement of natural walking itself rather than to changes in sensory input during walking. The results further indicate that the walking-induced modulation of ongoing occipital alpha oscillations drives the cognitive effects. We therefore suggest that walking changes the inhibitory state which can influence awareness and attention. Such a mechanism could facilitate an adaptive enhancement in cognitive processes and thereby optimize movement-related behaviour such as navigation.

Zusammenfassung

Menschen interagieren aktiv mit der Welt durch eine breite Palette von Körperbewegungen. Um die menschliche Kognition in ihrem natürlichen Zustand zu verstehen, müssen wir ökologisch relevante Körperbewegungen in unsere Betrachtung einbeziehen. Eine grundlegende Körperbewegung im täglichen Leben ist das natürliche Gehen. Trotz seiner Allgegenwärtigkeit ist die Auswirkung des natürlichen Gehens auf die Gehirnaktivität und die Kognition weitgehend unerforscht geblieben.

In der Elektrophysiologie haben frühere Studien eine robuste Reduktion der laufenden Alpha-Leistung im parieto-okzipitalen Cortex während Körperbewegungen gezeigt. Es war jedoch unbekannt, was die Reduktion des laufenden Alpha verursacht, nämlich ob dies auf Körperbewegung oder vorherrschende sensorische Eingangsänderungen zurückzuführen ist. Um dies zu klären, wurde Studie 1 durchgeführt, um zu testen, ob die Alpha-Reduktion von visuellem Input abhängig ist. Ich verglich die Alpha-Leistung im Ruhezustand beim natürlichen Gehen und Stehen, sowohl bei Licht als auch im Dunkeln. Die Ergebnisse zeigten, dass natürliches Gehen zu einer verminderten Alpha-Aktivität über dem okzipitalen Cortex im Vergleich zum Stehen führte, unabhängig von den Lichtverhältnissen. Dies legt nahe, dass die bewegungsinduzierte Modulation der okzipitalen Alpha-Aktivität nicht durch visuelle Veränderungen während des Gehens verursacht wird. Ich argumentiere, dass die beobachtete Reduktion der Alpha-Leistung eine Veränderung des Zustands der Versuchsperson aufgrund der durch das Gehen induzierten Hemmung widerspiegelt. Natürliches Gehen könnte daher die visuelle Verarbeitung und andere kognitive Prozesse, die die Aktivität des okzipitalen Cortex umfassen, verstärken.

Ich habe diese Hypothese zuerst im Bereich der Vision getestet. Studie 2 wurde durchgeführt, um die möglichen Auswirkungen des natürlichen Gehens auf verschiedene neurale Marker in verschiedenen Bewegungszuständen zu untersuchen. Die Ergebnisse zeigten eine verstärkte frühe visuelle Reaktion, während eine spätere visuelle Reaktion unverändert blieb. Eine Nachfolgestudie 3 replizierte die durch das Gehen induzierte Verstärkung des frühen visuellen ereigniskorrelierten Potenzials und zeigte, dass die Verstärkung von spezifischen stimuliabhängigen Parametern abhängig war (Exzentrizität, Lateralität, Vorhandensein von Störreizen). Die Ergebnisse lieferten wichtige Hinweise darauf,

dass die verstärkten frühen visuellen Reaktionen tatsächlich mit der Modulation der laufenden Alpha-Leistung im okzipitalen Cortex zusammenhängen. Das Gehen modulierte auch die stimuliinduzierte Alpha-Leistung. Insbesondere zeigte sich, dass bei Erscheinen des Ziels im fovealen Bereich ohne Störreiz das Gehen eine signifikant reduzierte Modulation der Alpha-Leistung aufwies und den größten Unterschied zum Stehzustand zeigte. Dieser Exzentrizitätseffekt deutet darauf hin, dass während späterer visueller Verarbeitungsstadien die visuelle Eingabe im Fovealbereich weniger verarbeitet wird als in peripheren Bereichen während des Gehens.

Die beiden visuellen Studien zeigten, dass Gehen zu einer Verstärkung früher visueller Prozesse führt, die durch die durch das Gehen verursachte Veränderung der laufenden Alpha-Oszillation wahrscheinlich markiert werden. Allerdings beeinflusst Gehen zwar neuronale Marker früher sensorischer Prozesse, führt aber nicht zwangsläufig zu einer Veränderung des Verhaltensergebnisses einer sensorischen Aufgabe. Die beiden visuellen Studien legen nahe, dass das Verhaltensergebnis hauptsächlich auf späteren Verarbeitungsstadien beruht.

Um die Auswirkungen des Gehens außerhalb des visuellen Bereichs zu testen, wandte ich mich in Studie 4 der Auditierung zu. Ich untersuchte den Einfluss des Gehens auf einen bestimmten Pfad im Vergleich zum einfachen Schritt auf die auditive Verarbeitung. Die Studie testete speziell, ob eine verbesserte Verarbeitung aufgrund des natürlichen Gehens in der primären auditorischen Hirnaktivität gefunden werden kann und ob die Verarbeitungspräferenzen vom Gehpfad abhängen. Darüber hinaus habe ich getestet, ob die in früheren visuellen Studien berichtete veränderte räumliche Verarbeitung auch im auditiven Bereich beobachtet werden kann. Die Ergebnisse zeigten eine verbesserte sensorische Verarbeitung aufgrund des Gehens im auditiven Bereich, die erneut mit der Modulation der okzipitalen Alpha-Oszillation in Verbindung stand. Die auditive Verarbeitung war auch vom Gehpfad abhängig. Darüber hinaus wurde eine verbesserte periphere sensorische Verarbeitung, wie sie in der Vision gefunden wurde, auch in der Auditierung beobachtet.

Die außerhalb des visuellen Bereichs gefundenen Ergebnisse unterstützen die Idee, dass natürliches Gehen die Kognition auf eher allgemeine Weise beeinflusst. Daher habe ich in meiner Studie 5 die Wirkung des natürlichen Gehens auf höhere kognitive Prozesse untersucht, nämlich das divergente Denken, und seine Korrelation mit der Modulation der

laufenden Alpha-Oszillation. Ich analysierte Alpha-Oszillationen und Verhaltensleistungen während eingeschränkter und uneingeschränkter Bewegungsbedingungen, während Versuchspersonen einen Guilford-Test für alternative Verwendungsmöglichkeiten absolvierten. Die Ergebnisse zeigten, dass natürliches Gehen sowie das Fehlen von Körperbeschränkungen die laufende Alpha-Leistung im okzipitalen Bereich unabhängig von der Aufgabenphase reduziert, was mit höheren Testergebnissen einhergeht. Die Reduktion der okzipitalen Alpha-Leistung kann daher ein Indikator für einen veränderten Zustand sein, der eine Verbesserung der höheren kognitiven Prozesse ermöglicht.

Zusammenfassend hebt die in dieser Arbeit präsentierte Forschung hervor, dass natürliches Gehen verschiedene Prozesse im visuellen und auditiven Bereich sowie höhere kognitive Prozesse verändern kann. Die Wirkung kann auf die Bewegung des natürlichen Gehens selbst zurückgeführt werden, und nicht auf Veränderungen im sensorischen Input während des Gehens. Die Ergebnisse deuten weiterhin darauf hin, dass die durch das Gehen verursachte Modulation laufender Alpha-Oszillationen im okzipitalen Bereich die kognitiven Effekte antreibt. Daher schlagen wir vor, dass Gehen den hemmenden Zustand verändert, der das Bewusstsein und die Aufmerksamkeit beeinflussen kann. Ein solcher Mechanismus könnte eine adaptive Verbesserung in kognitiven Prozessen fördern und somit verhaltensbezogene Bewegungen wie die Navigation optimieren.

1. General introduction

Humans constantly engage in a wide variety of body movements, from basic everyday actions to complex athletic behaviours. In order to execute those body movements, we rely on many cognitive processes. Accordingly, to understand cognition during natural behaviour, we need to take body movements into account and assess neural activity and related cognitive processes during movement execution.

In the following introduction, I will first explain why particularly ecologically relevant natural movement is important to consider (1.1). I will then review the experimental work on how body movement affects neural activity focusing on occipital alpha oscillations (1.2), and how body movements influence cognitive processes and their neural markers (1.3). Based on the review of existing work, I will introduce my open questions and my current project based on natural walking (1.4). In this project, I refer to "natural walking" as the walking wherein individuals use their body's musculoskeletal system with ecologically relevant purposes, such as going from one location to another.

1.1 The importance of considering ecologically relevant body movements to understand cognition

The investigations of human cognition have primarily been conducted using highly controlled sensory input on individuals in a stationary state, with maximal movement suppression. Such carefully designed experiments have played a crucial role in identifying and describing cognitive phenomena while minimizing confounding variables. However, there has been a growing recognition of the concept of embodied cognition, which emphasizes that cognitive processes are deeply intertwined with the body's interactions with the world (Byrge, Sporns, & Smith, 2014; Chiel & Beer, 1997; Grafton, 2009; Varela, Thompson, & Rosch, 1993; Wilson, 2002). An important way we interact with the environment is through body movement (Koziol, Budding, & Chidekel, 2012). Accordingly, as suggested by Gramann, Ferris, Gwin, and Makeig (2014), understanding the effects of concurrent body movement on cognitive processes is essential for advancing our understanding of human cognition.

A common strategy to investigate the impact of body movement on cognitive processes involves comparing behavioural performance between a resting state and a stationary engagement in body movement, such as treadmill walking or stationary cycling. These studies have yielded mixed results. Some reported a positive effect of body movement on cognitive tasks ranging from detection (Shields, Larson, Swartz, & Smith, 2011) and discrimination tasks (Sanabria et al., 2011) to more complex tasks like visual search (Brungart, Kruger, Kwiatkowski, Heil, & Cohen, 2019) or other higher level processes (Del Giorno, Hall, O'Leary, Bixby, & Miller, 2010; Rattray & Smee, 2016; Torbeyns et al., 2016). However, others have described a decline in cognitive performance during body movement compared to rest. Such movement-induced reduction in cognitive tasks was reported in detection tasks (Regnaux, Roberston, Smail, Daniel, & Bussel, 2006), discrimination tasks (Del Giorno et al., 2010; Regnaux et al., 2006), and higher-level complex cognitive tasks such as office work and problem-solving (Alderman, Olson, & Mattina, 2014; Dietrich & Sparling, 2004; John, Bassett, Thompson, Fairbrother, & Baldwin, 2009). Comparing specific experimental details, meta-analyses and reviews have proposed that the divergence regarding the impact of body movement on cognitive performance may depend on the specific cognitive task as well as movement type, intensity, and duration (Lambourne & Tomporowski, 2010; McMorris & Hale, 2012; Schmidt-Kassow & Kaiser, 2023; Wang, Chu, Chu, Chan, & Chang, 2013). In addition, whether such body movement is executed at a preferred speed can lead to a difference in facilitation or reduction of cognitive performance (Duncan, Smith, Clarke, Eyre, & Wright, 2016). Nevertheless, while it may be challenging to draw a general conclusion about how body movement influences cognitive behavioural performance, previous work suggested that cognition can be changed due to body movement.

Notably, despite the insights gained from studies based on stationary body movement, it is important to consider more natural body movements, e.g. natural walking or non-stationary cycling. First, movements such as stationary cycling or treadmill movements are biomechanically different from natural body movements. Take natural walking as an example, it was found that treadmill walking was different in both kinetics (why objects move the way they do) and kinematic aspects (how objects move) (for a review, see Riley et al., 2008; Semaan et al., 2022). Specifically, treadmill walking reduces the step length (Nagano, Begg, Sparrow, & Taylor, 2013), affects inter-limb coordination (Carpinella, Crenna, Rabuffetti, &

Ferrarin, 2010), modifies lower limb muscle activation patterns (Khademi-Kalantari, Rahimi, Hosseini, Baghban, & Jaberzadeh, 2017; Lim & Lee, 2018), and joint moments and powers (Lee & Hidler, 2008). These biomechanical differences between treadmill walking and natural walking can influence cognitive performance by altering the cognitive demands placed on individuals (Wrightson, Schafer, & Smeeton, 2020; Wrightson & Smeeton, 2017).

A second major distinction is the sensory input-related differences between stationary movement and natural walking. For example, natural walking produces full-field optic flow, a global pattern of visual motion, which is important for humans to guide their heading and interact with moving objects (Alefantis et al., 2022; Lee & Hidler, 2008; Niehorster, 2021; Warren, Kay, Zosh, Duchon, & Sahuc, 2001). However, this is absent during treadmill walking or stationary cycling. Furthermore, during natural walking, the auditory environment is rich and dynamic, and serves to provide valuable information for both perception and action during the movement (Camponogara, Turchet, Carner, Marchioni, & Cesari, 2016; Stroffregen & Pittenger, 1995). However, in treadmill-based experiments, the auditory input tends to be more monotonous and unaffected by changing ground and acoustic properties. In addition to the evident visual and auditory sensory input differences, there are sensory inputs that people may not even be aware of and are exclusive during natural walking or similar unencumbered movements. For instance, during natural walking, there is somatosensory input generated by the wind on the face (Seno, Ogawa, Ito, & Sunaga, 2011) as well as vestibular self-motion information (Angelaki, Gu, & DeAngelis, 2009), which improves the awareness of the surroundings and aiding in spatial orientation. Remarkably, the absence of the sensory inputs mentioned above during stationary movements can disrupt the closed loop between movement and sensory feedback (Roland, 1978). This loop plays a critical role in integrating sensory feedback with motor actions and influences how we perceive and interact with the world.

Lastly, there are some behavioural patterns and associated neuronal changes that can only be effectively observed and studied during natural walking. For instance, in real-world navigation, it is crucial to examine how route planning operates in dynamic scenarios and how attention shifts during specific actions like turning around. Animal studies have predominantly investigated spatial navigation and demonstrated the brain's construction of

unified representations of the environment, known as cognitive maps, which support memory and guide future actions (Grieves & Jeffery, 2017; O'Keefe & Dostrovsky, 1971). In humans, research on spatial navigation has primarily relied on virtual reality (VR) settings, however, as discussed by Händel and Scholvinck (2019), experiments in VR settings may not mimic all aspects of real-world navigation. Some basic information processes might be changed in VR settings. Understanding what genuinely occurs during natural walking is not only important to understand the cognition in the more ecological daily life background but also serves to assess the ecological validity of VR-based experiments.

In general, the consideration of body movement is fundamental for understanding human cognitive processes during natural behaviour. As reviewed above, I believe that particularly natural walking holds the key to unravelling ecologically relevant interactions between movement and cognition. My thesis therefore focused on investigating the influence of natural walking.

1.2 The influence of body movement on parieto-occipital alpha oscillations

According to the information processing model of cognition (Simon, 1979), human behavioural output is a result of multiple cognitive processes carried out by the brain. These processes encompass sensory processing, attentional selection, and higher cognitive functions such as reasoning and problem-solving, with interactions occurring among them (Luck & Ford, 1998; Simon, 1979). It is important to go beyond behavioural observations and study the neural measures that offer temporally precise insights into information processing. To better investigate the complex interactions between brain dynamics and body movement, wearable mobile brain/body imaging (MoBI) systems were proposed and developed in recent years (De Vos, Gandras, & Debener, 2014; Makeig, Gramann, Jung, Sejnowski, & Poizner, 2009). One such technology that has gained significant popularity in body movement-related research is the mobile electroencephalograph (EEG), commonly referred to as Mobile EEG. It is wireless, portable, and lightweight enough to be worn on the head. It has been utilized in numerous research endeavours to explore the relationship between brain activity and different aspects of movement (for reviews, see Ladouce, Donaldson, Dudchenko, & Ietswaart, 2016; Schmidt-Kassow & Kaiser, 2023). By analyzing neural signals such as the event-related potentials (ERPs) and brain oscillations, valuable insights into the nature of

different cognitive processes and how they are modulated by body movement could be obtained (De Vos & Debener, 2014; Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Gramann et al., 2011; Gwin, Gramann, Makeig, & Ferris, 2010; Makeig et al., 2009). The analysis of ERPs during body movements and their link to cognitive processes has led to valuable insights but overall showed continuously variable results (for a review, see Schmidt-Kassow & Kaiser, 2023). An exception is oscillatory activity, and particularly occipital alpha activity, which was very robustly reported to be modulated by body movements.

General introduction of alpha oscillations

Oscillatory activity in brain oscillations reflects rhythmic fluctuations of a population of neurons (Klimesch, Sauseng, & Hanslmayr, 2007). The alpha band oscillation over the occipital cortex, characterized by a frequency range typically between 8 to 14 Hz, is the most prominent oscillation. Its amplitude can be observed at a glance even in human scalp EEG and can be modulated by simply closing the eyes (Barry & De Blasio, 2017; Berger, 1929; Webster & Ro, 2020; Wostmann, Schmitt, & Obleser, 2020). Early research suggested that occipital alpha power increases when individuals are awake but not engaged in processing sensory input or executing motor tasks, a phenomenon known as cortical idling (Adrian & Matthews, 1934; Pfurtscheller, Stancak, & Neuper, 1996). A more modern view proposes occipital alpha oscillation to play an active role in cognitive processing. Specifically, it is suggested to mark a mechanism of functional inhibition. Low alpha activity is a signature of regions engaged in active neuronal processing, whereas strong alpha oscillations reflect the inhibition and disengagement of task-irrelevant cortical areas (for reviews, see Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch et al., 2007).

Perceptually we know that what sensory input will be inhibited and what will be less inhibited can be driven by attention (Posner, 1980). A typical example of the modulation of occipital alpha power is an observed power increase ipsilateral to the visually attended hemifield (Foxe & Snyder, 2011; Rihs, Michel, & Thut, 2007; Sauseng et al., 2005), marking the inhibition of the unattended stimuli. The strength of alpha inhibition ipsilateral to the task side indeed positively correlates with behavioural performance (Händel, Haarmeier, & Jensen, 2011). Alpha power might therefore be a marker of how intensely sensory input is

processed. The link between alpha oscillatory activity and attention will be further highlighted when discussing the influence of body movements on attention (1.3.4).

Please note that alpha oscillations are also prevalent in other cortical areas and linked to various cognitive processes besides attention. Previous studies have extensively examined alpha modulation in the sensorimotor cortex, which was found to be associated with the planning and execution of movement (Bulea, Kim, Damiano, Stanley, & Park, 2015; Peterson & Ferris, 2018; Storzer et al., 2016; Wagner et al., 2012; Wieser et al., 2010). Notably, alpha power can be also modulated by cognitive tasks without external sensory input change but with an internal process. For example, creative ideation (Fink & Benedek, 2014; Schwab, Benedek, Papousek, Weiss, & Fink, 2014), tasks involving imagination (Cooper, Burgess, Croft, & Gruzelier, 2006), and working memory (Jensen, Gelfand, Kounios, & Lisman, 2002; Sutterer, Foster, Serences, Vogel, & Awh, 2019; van Dijk, Nieuwenhuis, & Jensen, 2010), have all been shown to modulate alpha power. However, their experimental evidence is more likely to suggest an internally focused cognitive process.

For the work at hand, I distinguished between mainly three categories of modulation regarding alpha activity: (i) the modulation of alpha activity as a consequence of sensory input, which I refer to as event-related alpha, (ii) the modulation of ongoing alpha activity in preparation to specific task demands and, (iii) the fluctuation of ongoing alpha power due to internally governed processes. As the current project focuses on ongoing alpha oscillations in the parieto-occipital cortex and its relation to body movement, I will particularly review those studies investigating how body movement influences ongoing alpha oscillations during defined cognitive tasks, and how body movement affects ongoing alpha oscillations during cognitive rest. In addition, I will introduce some studies on the influence of body movement on alpha power modulation time-locked to a specific stimulus. Although this type of alpha power modulation due to sensory changes is not the primary focus of my research, understanding its relationship to ongoing alpha oscillations can provide valuable insights into the nature of the ongoing alpha power modulation by body movement.

1.2.1 Ongoing alpha oscillations

In the presence of a defined cognitive task

Several studies have reported modulation of ongoing alpha power by body movement in the presence of a specific task. The explanatory frameworks of alpha modulation due to movement while a second cognitive task is executed can be categorized into two main perspectives.

One perspective held the view that the alpha power modulations reflect alterations in the cortical processing of sensory input during body movement. For instance, Lin, Wang, Wei, and Jung (2014) found that the alpha power in occipital electrodes was reduced due to treadmill walking compared to standing when participants were asked to gaze at a visual flickering stimulus throughout the task. In this study, they assumed that the alpha power reduction might be related to the inhibition of idling activity because of increased sensory processing during walking. However, no specific evidence was provided. Another study showed an alpha power reduction in the parietal cortex while actively riding on an electric skateboard and performing an auditory task compared to a stationary state (Robles et al., 2021). Given that the stationary state served as a baseline condition without task-related stimuli, the authors also assumed that the observed reduction in alpha power was attributed to an overall increase in sensory input when riding on the skateboard. They proposed that this increase in sensory input, not only from the environment but also from the task itself, induced a general state of cortical excitability. This assumption also lacked clear experimental evidence to support it. Notably, in a study conducted by Cao and Händel (2019), the occipital alpha power reduced during free natural walking compared to standing was further reported to be positively correlated with the steady-state visual evoked potential (SSVEP) power. The SSVEP was more strongly modulated by the surrounding contrast during walking compared to standing, providing evidence that the alpha power reduction might be a result of a comparatively disinhibited processing of peripheral input during walking.

Another set of studies has discussed the modulation of alpha power due to body movements as a result of cognitive-motor interference. For instance, using an auditory oddball task, Kuziek, Redman, Splinter, and Mathewson (2018) observed a decrease in parietal alpha power during stationary cycling compared to sitting. They proposed that the decrease of alpha power while biking was likely due to the dual task of having to focus on the pedaling speed while also maintaining fixation to a central fixation cross. A similar reduction

of alpha power, in an auditory task was also found while non-stationary cycling freely outside compared to paddling on a stationary bike (Zink, Hunyadi, Huffel, & Vos, 2016). The authors analyzed the alpha power based on target trials and therefore considered the reduction to be caused by the increased task difficulty in real-life circumstances and the physical engagement of body movement. However again, no further evidence was provided to support this proposal in these two studies. Several studies have reported a decrease in upper band alpha power during walking compared to a stationary state when using a visual discrimination task (Nenna, Do, Protzak, & Gramann, 2020; Shaw et al., 2018). Particularly, in Shaw et al. (2018)'s study, they found that the same alpha power that was modulated by body movement was also modulated by task difficulty. This led the authors to propose that the modulation of alpha power might reflect the allocation of attentional resources in motor-cognitive dual-task experiments. However, it is important to note that these studies observed a reduction in alpha power across multiple cortical regions, including the frontal, parietal, and occipital cortices. We should refrain from further interpreting the alpha power reduction as a specific parieto-occipital effect.

Overall, the alpha reduction due to body movement during a consecutive cognitive task could be seen as a robust finding. It has been explained by either a change in cortical processing of sensory input during walking or as result of reduced cognitive resources. However, previous scholars only provided an interpretation without grounding them in clear experimental evidence.

In the absence of a defined cognitive task

There is further evidence that body movement influences occipital alpha power independent of specific concurrent cognitive tasks but during cognitive rest. In the study mentioned above by Lin et al. (2014), the reduction of occipital alpha power during treadmill walking compared to standing was also observed when no specific visual stimulus was presented. Ehinger et al. (2014), using a VR setup, found that alpha power in the parieto-occipital cortex was reduced during active walking compared to standing. Moreover, the power showed a stronger decrease during turning movements compared to straight walking. The authors proposed that the decrease in alpha activity reflects heightened sensory processing and increased cortical excitability. Scanlon, Townsend, Cormier, Kuziek, and

Mathewson (2019) showed reduced alpha power in the parietal cortex during outside cycling compared to sitting in a chamber. They proposed that it was the multitude of visual, auditory, and other sensory information during movement outside that led to the reduction of alpha power compared to the indoor environment (Scanlon et al., 2019). However, a later study did not support that the alpha power reduction was simply because of increased sensory input. Vaughn et al. (2021) found a decrease in occipital alpha power during outdoor cycling compared to simply sitting outside. This finding is noteworthy as it suggests that the reduced alpha power during movement is not primarily due to the massively increased sensory input from the external environment. As the study ensured similar sensory stimulation in the cycling condition and driving condition, it provides evidence against the idea that changed external sensory input is the driving force of the decreased alpha power during body movement. Furthermore, Vaughn et al. (2021) observed that alpha power was decreased during outdoor cycling compared to driving. The act of driving and cycling involves distinct ways of moving the body; one involves active body movement while the other can be seen as a relatively stationary body state. This result might indicate that it was not the changes in sensory input, especially the prevalent visual input changes that changed the ongoing alpha power modulation. They emphasized the importance of the body movement itself.

In summary, the reduction of alpha power during body movement in the parieto-occipital cortex was robustly observed independent if a cognitive task was presented or not. This suggested that the alpha modulation due to movement marks a more general neural change. However, if and how the movement-induced change of ongoing alpha power in the parieto-occipital cortex affects cognitive processes is still unclear. Similarly, while it has been shown that the effect of walking on alpha is independent of a specific visual task, it was not excluded that the overall visual input during walking drives the neural modulation of alpha.

1.2.2 Event-related alpha oscillations

Researchers have analysed the influence of body movement on parieto-occipital event-related alpha power as a measure of specific task-related cognitive processing. This specifically refers to the alpha oscillatory activity that is time-locked to specific events or stimuli during an experiment. While the number of these studies is limited, they have revealed diverse findings.

Several studies have reported null results. For instance, in a task-switching paradigm involving a cue and a stimulus tone in each trial, Reiser, Wascher, Rinkenauer, and Arnau (2021) analysed the occipital cue-induced and stimulus-induced alpha oscillations. They did not observe any significant differences in either cue-induced or stimulus-induced alpha power between standing and walking conditions. Similar null results were also reported in studies involving participants of different age groups and those with Parkinson's disease, performing an auditory oddball task during treadmill walking or standing (Possti et al., 2021).

In some tasks, there was a positive influence of body movement on the event-related alpha power. Peskar et al. (2023) observed a higher stimulus onset induced alpha power in the central-parietal cortex during walking compared to standing using various Stroop tasks, including word reading, ink-naming, and instructions switching. They suggested that increased event-related alpha power may reflect facilitated selective attention. However, they did not find a corresponding behavioural improvement in walking, nor did they provide additional evidence supporting a direct relationship between the observed alpha power changes and attention.

More complex results were found in a study by Bradford, Lukos, Passaro, Ries, and Ferris (2019) during a visual oddball task comparing treadmill walking and sitting. They compared the event-related alpha power in distinct time windows that locked to the visual target onset separately. In one time window, they observed a reduction in alpha power during walking, while in the other time window, they observed an increase in alpha power during walking. The overall accuracy was lower during sitting compared to walking; however, the study did not provide further correlational evidence to investigate the specific implications of the event-related alpha power modulations due to walking in these different time windows.

Overall, the literature on a body movement-related modulation of stimulus event-related alpha shows diverse results. This variability can be attributed to several factors, including variations in experimental paradigms, task conditions, and cognitive processes being examined. Despite the challenge of drawing a general conclusion based on these diverse findings, a potential implication is that the movement-based modulation of event-related alpha power is not related to the modulation of ongoing alpha power. The modulation of ongoing alpha power and event-related alpha power might reflect different aspects or

different stages of information processing, which are affected differently by body movement. To illuminate the meaning behind these modulations, it is essential to consider how body movement influences cognition in combination.

1.3 The Influence of body movement on cognition

To further understand the interaction between body movement and cognition, I primarily review EEG studies that provide neural and behavioural evidence on how body movement influences different stages of information processing. I am mainly interested in sensory input processing, perceptual outcomes and higher-level cognitive processes. I will also review how attention is modulated by body movement across diverse cognitive processes.

1.3.1 Neural marker of sensory processing

General cortical sensory processing

Electrophysiological research in animal models has revealed that body movement can lead to amplified neural responses in the primary visual cortex (Ayaz, Saleem, Scholvinck, & Carandini, 2013; Niell & Stryker, 2010; Vinck, Batista-Brito, Knoblich, & Cardin, 2015). These findings suggested enhanced cortical sensory information processing associated with body movement (Busse, 2018). In human studies, the exploration of the impact of body movement on sensory processing has been limited in terms of quantity. However, there is compelling neural evidence that indicates a modification in sensory processing due to body movement.

Concerning auditory tasks, a study by Scanlon et al. (2019) showed that cycling outside significantly increased the auditory N1 amplitude. This effect was observed in response to both standard (non-target) and target stimuli, indicating an enhanced general sensory processing due to body movement. However, in this study they attributed this enhancement to the abundance of sensory input from the external environment, thus potentially underemphasizing the role of body movement. A recent study with conditions including non-stationary cycling and driving, as well as a physically stationary condition where participants sat outside, examined the neural marker of sensory processing known as the MMN (Mismatch Negativity) (Vaughn et al., 2021). They showed that the MMN amplitude was larger during non-stationary cycling compared to both driving and sitting. These results challenge the

assumption that the cortical sensory processing enhancement observed during non-stationary cycling was due to increased sensory input because of environmental change. This study additionally showed that the MMN was stronger during non-stationary cycling compared to driving, suggesting that rather natural body movement has a significant impact on sensory processing. In contrast, during driving, where the body is relatively static or minimally moving, the enhancement in sensory processing was not as pronounced.

Although some studies have provided evidence of modulated early ERPs as neural markers of changed early sensory processes, many others did not observe a significant increase in early sensory evoked components (Debener, Minow, Emkes, Gandras, & De Vos, 2012; Garrett, Bullock, & Giesbercht, 2021; Gramann et al., 2010; Malcolm, Foxe, Butler, & De Sanctis, 2015; Shaw et al., 2018). The discrepancy between studies, as highlighted by Garrett et al. (2021), may be ascribed to differences in the data collected. Specifically, studies that reported an enhancement in early ERPs during body movement (e.g., N1 component in Scanlon et al. (2019) exhibited an amplitude of around or stronger than 3 mV. Conversely, studies that failed to find such an enhancement typically had comparably lower amplitudes during rest (Garrett et al., 2021; Malcolm et al., 2015; Nenna et al., 2020). This suggested that a low signal-to-noise ratio could have masked the effect in studies with lower amplitude responses. Are there any other factors, such as the execution of the body movement? The body movement performed in Scanlon et al. (2019)'s research is a non-stationary real outside cycling, which can be seen as a natural body movement. Also in the study by Vaughn et al. (2021), the amplitude of the neural marker of temporally early sensory processes (the MMN component) was stronger during outdoor non-stationary cycling compared to sitting and driving. The non-stationary cycling could also be viewed as a natural body movement. These findings suggested that natural body movement could potentially serve as an important factor to unveil more pronounced effects on cortical sensory processing.

Overall, it is important to emphasize that even though only a minority of studies showed evidence of enhanced early visual ERPs, indicating heightened sensory processing due to body movement, the presence of this enhancement is still noteworthy. Nevertheless, it is plausible that the modulation of neural markers of general cortical sensory processing is so sensitive to the experimental set-up that it can only be discerned under highly naturalistic

conditions, such as during natural walking. This limitation not only reflects the genuine circumstances encountered in real-life scenarios but also has the potential to address concerns regarding statistical power.

Sensory input and task-specific sensory processing

The above-reviewed studies indicated that body movement can, under specific circumstances, lead to changes in general cortical sensory processing. Some studies have provided neuronal evidence indicating that certain sensory inputs and task-specific sensory processing can also be influenced by body movement.

In terms of sensory input-specific processing, there was evidence suggesting that body movement can lead to spatially specific changes in sensory processing. Cao and Händel (2019) found that the pre-target-induced SSVEP was more strongly modulated by the surrounding contrast during walking compared to standing, suggesting changed spatial processing during natural body movement. Innovatively, Cao and Händel (2019) proposed that the increased processing of peripheral visual input during walking was associated with altered inhibitory processes. This assumption was indicated by the positive correlation between ongoing alpha oscillations and the changes in SSVEP amplitude. Using a contrast discrimination task, Benjamin, Wailes-Newson, Ma-Wyatt, Baker, and Wade (2018) also showed that detection/discrimination thresholds were higher during walking than during a stationary condition when visual stimuli were presented with surrounding gratings. The behavioural indication of a surround suppression was supported by an increased SSVEP contrast response accordingly. Their findings indicated an enhancement in spatial-specific contrast processing and suggested an increased spatial surround suppression during treadmill walking. A recent study by Reiser, Arnau, Rinkenauer, and Wascher (2022), using a single-stimulus visual detection paradigm, further supported the idea of changed spatial sensory processing. When analysing the second peak of the N1pc/N2pc complex, they observed a reduced N2pc latency in walking compared to stationary states, but only in the extrafoveal stimulus eccentricity condition. This finding was interpreted as evidence of a faster re-entrant processing of stimuli with diminished saliency during walking. Notably, changed spatial sensory processing during body movement has not been reported in the auditory domain.

In addition to changes in spatial-specific sensory processing, body movement has been reported to influence task-specific sensory processing. In a visual oddball task, Bullock, Cecotti, and Giesbrecht (2015) found that during low-intensity exercise, the visual parieto-occipital early P1 component in target trials peaked significantly earlier compared to rest and high-intensity exercise. This finding suggested that body movement influences the sensory processing specifically related to the target. Additionally, they found that the amplitude of the P1 component, induced by the non-target standard stimulus only, was stronger during low-intensity exercise compared to rest conditions. This implied that the amplitude enhancement of the P1 component, and the associated process during low-intensity exercise was also task-specific. Notably, as both task-specific sensory enhancement was observed in low-intensity exercise, the researchers proposed there might be an ideal level of exercise necessary for optimal sensory gain and more rapid processing. This assumption was later supported by further evidence using SSVEP, showing that feature-selective tuning profiles were highest during low-intensity exercise (Bullock, Elliott, Serences, & Giesbrecht, 2017). Another study by Dodwell, Liesefeld, Conci, Muller, and Tollner (2021) compared the visual positivity posterior contralateral (Ppc) component, which is induced by the most salient item (in their study, the distractor) within the salience map between movement states. They found that the Ppc amplitude was significantly stronger during moderate exercise when compared to rest and vigorous exercise. Although the exact cause for the emergence of the Ppc component remains somewhat unclear, it is often associated with stimuli of high salience. In this context, the Ppc component enhancement induced by salient stimuli during exercise can be considered as reflecting the detection and prioritization of relevant sensory information. Moderate exercise may lead to an increased sensitivity and responsiveness of the sensory system to salient stimuli.

1.3.2 The perceptual outcome

Given the fact that sensory processing and perception are closely intertwined processes (Klemen, Buchel, & Rose, 2009; Mangun & Hillyard, 1991; Sorensen, Bohte, Slagter, & Scholte, 2022), the influence of body movement on sensory processing raises the question of whether such changes manifest as observable behavioural outcomes in perception. Indeed, there have been some studies reporting that perception is influenced by body movements. I will specifically address behavioural results from detection tasks, where participants solely

report the presence of a stimulus without undertaking a discrimination or interpretation process.

The possible cognitive-motor interference would predict a detrimental effect of body movement on perceptual processing (for a meta-analysis see Al-Yahya et al., 2011). Although there were reports of a negative influence of body movement (Ando, Kokubu, Kimura, Moritani, & Araki, 2008; Brisswalter, Arcelin, Audiffren, & Delignieres, 1997; Paas & Adam, 1991), it is intriguing that many findings did not support such impairment due to body movement. This has been observed in numerous studies utilizing a simple detection task based on an oddball paradigm, where participants were specifically instructed to detect a target by pressing a handheld button. They have consistently reported that body movement did not slow down the speed to detect targets compared to stationary states (Bradford et al., 2019; De Sanctis, Butler, Malcolm, & Foxe, 2014; Robles et al., 2021). Body movement led to a negative perceptual outcome only under specific circumstances dependent on the experiment. For instance, Protzak, Wiczorek, and Gramann (2021) conducted a simple stimulus detection task and found that the number of missed visual stimuli was similar between walking and sitting or standing for the younger participants. It was only for older participants, that they missed more stimuli during walking as compared to stationary states. Similarly, there were no differences in both reaction time and accuracy between normal walking and standing when detecting a visual target stimulus. A slower reaction time was only observed when gait was perturbed.

In addition to those studies reporting no significant negative effect of body movements on perceptual behavioural measures, several studies even reported beneficial effects on perceptual outcomes due to body movement. For instance, it was found that the speed of perceiving and detecting visual and auditory targets was faster during body movement compared to a stationary state (Bullock et al., 2015; Yagi, Coburn, Estes, & Arruda, 1999). Bradford et al. (2019) reported a higher accuracy during walking than sitting in a visual detection task. Body movement has also been reported to have favourable effects on some specific aspects of perception. For example, body movement has been shown to enhance visual perception in tasks related to motion perception. Research indicated that individuals who are actively walking or engaged in rhythmic movements exhibit improved sensitivity to

visual motion stimuli compared to those who are stationary and only watch a scene of simulated self-motion (Dokka, MacNeilage, DeAngelis, & Angelaki, 2015; Layton, Parade, & Fajen, 2022; Xie, Niehorster, Lappe, & Li, 2020). Moreover, body movement can also influence spatial perception. Benjamin et al. (2018) found the detection thresholds for contrast changes higher during treadmill walking compared to a stationary state in targets masked with an annular surround. This effect of body movement was not observed for targets without a surround mask, suggesting that walking may facilitate perceptual performance when there are changes in spatial demands. Cao and Händel (2019) reported that peripheral visual processing was enhanced during walking, as evidenced by a smaller difference in detection threshold between natural walking and standing conditions for peripheral targets compared to central targets.

In summary, research showed ample evidence that body movements do not have a general negative effect on perception, but in many cases can enhance the perceptual outcome. However, it is crucial to avoid making generalizations about the absolute positive or negative effects of body movement, as various factors seem to play a role. One significant factor is the influence of movement speed in modulating perception (Kurosawa, 1994; Richer, Polskaia, Raymond, Desjardins, & Lajoie, 2019). It appears that body movement only aids perceptual behavioural performance within a certain range of speed, which is dependent on specific experimental settings. In addition, how a specific perceptual process is changed during body movement can depend on its relevance to the specific motor output being executed. One can also assume an enhanced spatial perception, namely improved peripheral processing might also be particularly important for more ecologically relevant natural walking. Ideally, studying natural body movements, particularly those that closely mimic real-life scenarios, such as natural walking, holds the key to uncovering ecologically relevant interactions between movement and cognition.

1.3.3 The higher cognitive processes-creative thinking

The investigation of body movement's influence on sensory processing and perception led to a growing interest in the possible relationship between body movement and higher-level cognitive processes such as critical thinking, problem-solving, and decision-making (for a review, see Schmidt-Kassow & Kaiser, 2023). For the current thesis, I specifically focus on

creative thinking, encompassing both divergent and convergent thinking processes (Guilford, 1967), as previous studies have shown robust effects. A review, by analyzing published manuscripts (while not used meta-analytic approach), has concluded an overall positive association between body movement (in various intensities and durations) and creative thinking (Frith, Ryu, Kang, & Loprinzi, 2019). However, there are two things that are interesting to note.

First, most research indicated a positive influence of body movement on divergent thinking, promoting the generation of multiple ideas and exploration of alternatives. However, the effects on convergent thinking, involving selecting the best solution out of multiple possibilities, are less conclusive. Some studies suggested that body movement did not have any benefit or even a negative impact (Frith & Loprinzi, 2018; L, Szapora, Pannekoek, & Hommel, 2013). To be more specific, Oppezzo and Schwartz (2014) found that both walking indoors and outdoors led to improved divergent thinking, suggesting that walking, rather than being outdoors drives a positive effect on creativity. However, they also reported that the task performance in convergent thinking was not influenced by walking. A similarly exclusive positive influence of walking on divergent thinking was reported in studies by Abdullah, Czerwinski, Mark and Johns (2016). Besides walking, the divergent thinking improvement was also found to be elevated due to vigorous stationary cycling (Chen, Mochizuki, Hagiwara, Hirotsu, & Nakagawa, 2021), or VR-based movement on a train (Fleury et al., 2020) while no effect was found on convergent thinking (Chen et al., 2021). A very interesting study by Matsumoto et al. (2021), although it did not measure the congruent performance but the performance shortly after the body movement, revealed that compared to using an elevator, stair-climbing led to an improvement in divergent thinking but not in convergent thinking.

Second, for divergent thinking, many findings suggested that it is the unrestricted body movement that aids task performance. One component of such an unrestricted state includes a ‘free’ body movement path. Leung et al. (2012) showed that participants who walked freely performed better on divergent thinking than participants who walked along a rectangular path. Kuo and Yeh (2016) also showed that participants exhibited better performance when engaging in free walking compared to walking along a prescribed rectangular path. The authors additionally tested whether the effect was due to the path

which induces a metaphorical concept of constraining one's thoughts. They included a condition where participants had to walk in a path that was generated during another participant's free walking. They found that performance was improved only during the actual free walking. These findings addressed the importance of real unrestricted movement in influencing divergent thinking. In addition to the unrestricted path, maintaining a free and natural pace is also crucial. The positive influence of treadmill walking on divergent thinking was actually based on the fact that participants walked at a natural pace (Oppezzo & Schwartz, 2014). Moreover, small changes in body posture, i.e. the way participants were seated, can also influence the level of creativity (Andolfi, Nuzzo, & Antonietti, 2017). Specifically, sitting in a more natural posture led to a better performance compared to a more constrained posture.

What are the potential explanations for the observed improvement in divergent thinking tasks when individuals engage in free body movement? Radel, Davranche, Fournier, and Dietrich (2015) have shown that experimentally depleting cognitive resources through the inclusion of secondary tasks improved performance in the divergent thinking task. Building on this, Zhou, Zhang, Hommel, and Zhang (2017) discussed that the reduced cognitive resources could explain performance when standing up while keeping balance than when lying or sitting. They assumed that standing up and keeping balance was the most depleting condition and exhausted the most control resources therefore improving ideas generation. However, as argued by Murali & Händel (2022), it is not obvious that following instructions during restriction would involve fewer cognitive resources than unrestricted movement. Indeed, the additional task during restricted walking could be viewed as more challenging. The finding of better task performance in unrestricted walking compared to the unrestricted state in their specific task can be viewed as contrary to the proposed idea of reduced cognitive resources improving divergent thinking.

Interestingly, Murali and Händel (2022) proposed that the improvement in divergent thinking during free body movement was not dependent on the amount of cognitive or attentional resources, but rather on the distribution and size of attentional focus. In fact, the general influence of attentional focus on divergent thinking has received many support in previous studies. For example, it was found that creative individuals tend to have a broader

attentional focus than less creative individuals (Dykes & McGhie, 1976; Martindale, 1999; Mendelsohn & Griswold, 1964, 1966). Attention broadening training can also enhance creative performance (Memmert, 2007). In addition, manipulating attentional focus to include larger visual areas, such as attending to bigger stimuli (Nijstad, De Dreu, Rietzschel, & Baas, 2010), or presenting stimuli in the periphery rather than just the fovea (Friedman, Fishbach, Förster, & Werth, 2003), led to improved performance on divergent thinking tasks.

Regarding the improved performance during free body movement, Murali and Händel (2022) suggested that there was an expanded attentional focus during free movement, which positively influences divergent thinking. This idea of expanded attention has been mentioned before considering the improved divergent thinking during movement; for instance, Abdullah, Czerwinski, Mark and Johns (2016) proposed that the exclusive effect of body movement on divergent thinking was due to attentional states differentially affecting these two aspects of creativity. For convergent thinking, focused attention is needed; however, divergent thinking might rather require defocused attention, which is supposedly differently modulated by body movement. Andolfi et al. (2017) did not find any difference in physical discomfort between restricted or unrestricted states, and they suggested it is more likely that the broader mental framework during an unstrained state allows individuals to let their thoughts wander freely. This freely wander helps to find various answers to the divergent thinking task. However, neurological evidence to support this broadened attention proposition has not yet been provided.

Overall, previous work has shown that divergent thinking is improved during unrestricted movement. This was discussed in the light of changed attentional focus. A largely open question is the neural changes introduced by movement that lead to improved creativity. For example, the robust modulation of ongoing alpha activity due to body movements has not been correlated with higher cognitive- behavioural effects.

1.3.4 Attention

In addition to specific processes such as sensory processing, perception, and divergent thinking, some fundamental processes significantly influence both cognitive processes and behavioural outcomes. One particular relevant process is attention, which plays a crucial role

in filtering and selecting relevant information from the environment or a task (Driver, 2001; Jonston & Dark, 1986). There were quite some studies that have investigated or discussed how body movement affects neural markers of attention. Researchers have focused on both ERPs and alpha oscillations as indicators in this area of investigation.

ERPs and behavioural changes based

The studies inspecting ERPs mainly focused on attention directed toward external task-related stimuli, with a specific emphasis on task-relevant features such as location or colour. Different studies have revealed different results regarding how body movement modulates such selective attention-related ERPs.

Many studies suggested that motor-cognitive interference led to more attentional resources being allocated to the motor task. This resulted in a reduction of attention available for the cognitive task (for a review, see Leone et al., 2017). For example, using auditory oddball tasks, many have shown reduced P300\N2 amplitude evoked by a stimulus, accompanied by a decreased behavioural performance in discrimination and detection (De Vos et al., 2014; Ladouce, Donaldson, Dudchenko, & Ietswaart, 2019; Olson et al., 2016; Reiser et al., 2021; Shaw et al., 2018). These findings aligned with previous research that has established ERPs as well-recognized neural markers of attentional effects (for a review, see Polich, 2007). Authors usually interpreted their findings such that body movement led to divided or reduced attention. Similar findings were also found using a visual oddball task. Protzak and Gramann (2021) found a reduced P300 amplitude during walking compared to standing, with a slower reaction time found during walking. These findings are consistent with the conclusion from Yagi et al. (1999), showing that both auditory and visual P300 amplitudes and error rates were decreased during exercise, suggesting diminished attentional resource allocation across modalities.

However, others have reported beneficial effects of body movement. Yagi et al. (1999) found that paralleling the reaction time changes with oddball task performance, auditory and visual P300 latencies were decreased during exercise. They proposed that this indicated a faster cognitive information processing in both sensory modalities during body movement. Similarly, Bullock et al. (2015) showed that the visual P300 component latency peaked

significantly earlier during stationary cycling compared to the resting state, and the reaction time was also significantly decreased during cycling in the oddball task. They assumed faster cognitive information processing during cycling, which was based on a faster attention allocation. A clearly faster reaction time pattern was also reported during moderate cycling compared to rest, although it did not reach statically significance (Dodwell, Liesefeld, Conci, Muller, & Tollner, 2021). Their neural marker of attentional selection, named the PCN component (similar to the N2pc component), also had a smaller latency during moderate cycling.

To be noted, some research has highlighted the significance of considering motor task execution when evaluating the effects of body movement. Torbeyns et al. (2016) demonstrated that people can work on a bike desk with equal typing performance and short-term memory tasks compared to sitting, with no difference between the P300 and other cognitive process-related neural markers. Similarly, Robles et al. (2021) reported no significant difference in P300 component amplitude and behavioural performance between an electric skateboarding condition and a resting stationary state. In the electric skateboarding condition, participants engaged in light riding on an electric skateboard. It is possible that this type of movement was highly specialized, requiring the body's engagement to maintain balance while moving forward, yet the propulsion force did not originate from the body. Such movement might demand a comparable level of focus as activities like driving or even remaining stationary. Nevertheless, these studies have pointed out that motor execution might play a crucial role in modulating attention-related processing. Different motor executions can lead to different motor task demands in cognitive-motor interference. The factor of motor execution might also explain why Scanlon, Sieben, Holyk, and Mathewson (2017a) did not find any difference in the P300 component between stationary cycling and sitting but in a later study, a decreased P300 amplitude (Scanlon et al., 2017b) and decreased P2 component in a real and natural outdoor cycling compared to sitting was observed (Scanlon et al., 2019). They have discussed that body movements such as stationary cycling do not require a great deal of focused attention, especially when indoors. Their assumption in such way potential mean a broadened attention during natural movement compared to stationary cycling.

Alpha oscillation based

In addition to examining ERPs, researchers have also investigated the influence of body movement on attention by analysing the modulation of parieto-occipital alpha power. This investigation encompassed the study of both ongoing alpha oscillations and event-related alpha oscillation.

Some studies found a modulation of ongoing alpha oscillation when participants were moving while engaging in a visual or auditory task. The reduced ongoing alpha power during walking was interpreted as evidence of decreased attentional resources due to cognitive-motor interference (Kuziek et al., 2018; Nenna et al., 2020; Zink et al., 2016). However, this interpretation was merely based on the general link between alpha power and attention. Only in Shaw et al. (2018)'s study, they found a decrease in ongoing alpha oscillation during walking compared to stationary states. As the same alpha power was also found to be reduced with increased cognitive task difficulty, the authors proposed that the modulated alpha power reflects less attentional resources in motor-cognitive dual-task experiments. However, the reduction in alpha power was found in multiple cortical regions, including the frontal, parietal, and occipital cortices. It can therefore not be concluded that it was a specific parieto-occipital effect. It is worth noting that alpha power increases during creative ideation were considered to reflect more internally oriented attention (for a review, see Fink & Benedek, 2014). When exploring the influence of body movement on attention, attention-based mechanisms have also been proposed (Abdullah, Czerwinski, Mark, & Johns, 2016; Andolfi et al., 2017; Murali & Händel, 2022). However, how the ongoing alpha oscillation modulation during walking is linked to such higher cognitive processes remains unclear, as I have also reviewed above (1.3.3).

Some studies found a modulation of event-related alpha oscillation due to body movement. Using factorial ANOVA, Peskar et al. (2023) showed that the Stroop stimulus-induced parietal alpha power was significantly more decreased in the task that exhibited the highest Stroop effect (along with the slowest reaction time). This observation suggested that more attentional resources were likely required and utilized in the most challenging Stroop task. Interestingly, the factorial ANOVA also showed a main effect of body movement, namly the central- parietal alpha power was more strongly reduced during sitting compared to standing.

This result hints at the possibility that increased attentional resources are allocated when individuals are in a seated position. However, some studies examining event-related alpha power with a focus on attention did not find an influence of body movement. Reiser et al. (2021) conducted an experiment based on a task-switching paradigm with both a cue and auditory stimulus in each trial. They expected that event-related alpha would reflect modulated attention with changed movement complexity. However, they did not find any differences in occipital alpha power between all movement conditions, regardless of whether it was induced by the cue or the stimulus. The accuracy was also found to be comparable between different movement states.

To summarize both ERPs and alpha-related studies, the divergent findings from the variable experimental set-ups suggested that the effect of body movement on attention is complex. It is difficult to arrive at a general conclusion regarding how body movement influences attention. Firstly, the effect of body movement seems to be dependent on the specific movement execution. Secondly, the effect seems dependent on the specific type of cognitive task that is used to test the attentional change. In addition, as there are different neural markers of attention, such as the latency or amplitude of the P3 component and oscillatory activity. The broad variety of findings gives a complex picture that is hard to interpret. Investigations that take all known neural markers as well as behavioural markers in one defined task into account might help to increase our understanding of the complex influence of body movement on attentional processes.

1.4 The open questions and overview of the presented work

By reviewing the studies showing an influence of body movement on occipital alpha oscillations (1.2), a robust observation emerges regarding ongoing alpha oscillations: many studies have reported a decreased alpha power during movement, regardless of whether participants were engaged in a cognitive task or while at rest. However, what caused the reduction of ongoing alpha power during body movement compared to a stationary state was unclear. A specific open question is if visual input drives the reduced ongoing alpha power due to body movement.

To test if the ongoing alpha oscillation modulation by natural walking is independent of visual input, study 1 was performed. I recorded the resting state alpha power during free walking and standing, in both light and darkness. I found that natural walking led to decreased alpha activity over the occipital cortex compared to standing, regardless of the lighting condition. This suggested that the movement-induced modulation of alpha activity is not driven by the visual input. It was further excluded that the modulation was based on eye movements or electrode impedance.

Given that alpha power has been functionally linked to inhibition, I interpreted the observed reduction as a disinhibition of the occipital cortex. Does the disinhibition in the primary visual cortex influence visual processing? I specifically focused on both temporally early visual sensory processing and later visual processing stages as well as the behavioural outcome. As the reduction of ongoing alpha oscillation was independent of visual input changes, I further asked if this disinhibition enhances not only visual processing but also extends to processes beyond vision, such as auditory processing, or any cognitive activities involving the occipital cortex. To further understand how natural walking changes occipital ongoing alpha oscillations and concurrently modulates cognitive processing, I investigated the influence of natural walking on cognition in various domains, including visual, auditory, and higher cognitive processes. A further aim was to establish the cognitive correlates of the modulation of occipital alpha power by natural walking.

Study 2 was performed to understand the influence of walking on different visual processing stages. Specifically, to confirm the enhancement of early sensory responses as indicated by animal models and in humans. To this end, I compared the neural markers of different stages of processing in a line orientation discrimination task between natural walking and standing. The results showed an amplified temporally early visual response during walking, while the later visual response was comparable between movement states. The results suggested that walking has differential effects across visual cortical processing stages.

Study 3 mainly aimed to establish a link between the modulation of ongoing alpha oscillation and sensory input processing due to natural walking. By further manipulating the stimulus parameters (eccentricity, laterality, distractor presence) of the paradigm used in

study 2, I tested first the relationship between pre-stimulus alpha, stimulus-induced alpha, and early ERPs and second, the dependence of these neural markers on stimulus parameters. The results showed a stimulus-independent enhancement in temporally early sensory processes due to walking, which could be predicted by ongoing pre-stimulus alpha oscillation. Walking also modulated the stimulus induced alpha power but this was dependent on stimulus-related parameters such as eccentricity. It indicated enhanced peripheral processing, but this modulation was not linked to the ongoing occipital alpha modulation.

In study 4, I investigated whether the enhanced general sensory processing due to walking can also be found in the auditory domain. I also tested if the modulation is dependent on the direction of the walking path. Additionally, I examined whether a spatially specific sensory processing enhancement for peripheral input can be found in auditory processing comparable to findings in visual processing. To this end, I tested for a link between ongoing alpha oscillation, an auditory steady-state response (ASSR), and ASSR perturbation (central vs. peripheral). The results provide evidence for a walking-induced change in general sensory processing and enhanced peripheral sensory processing in the auditory domain. However, only the general sensory processing enhancement was linked to the modulation of ongoing alpha oscillation due to walking. Additionally, the results showed that there is a modulation of auditory processing dependent on the walking path.

In study 5, I examined the modulation of ongoing alpha oscillation due to movement and its link to higher cognitive processes, namely divergent thinking. To this end, behavioural and alpha oscillation data were recorded during restricted and unrestricted movement conditions while subjects completed a Guilford's alternate uses test. Ongoing alpha power, which was modulated due to movement and movement restriction, was positively correlated with the generation of divergent ideas but not confined to the time when ideas had to be generated. This study suggested that movement such as walking as well as missing movement restriction reduces the ongoing occipital alpha power, which can be an indicator of a changed state that also affects higher cognitive processes.

2. Study 1: Overground walking decreases alpha activity and entrains eye movements in humans

Overground Walking Decreases Alpha Activity and Entrains Eye Movements in Humans

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Abstract:

Experiments in animal models have shown that running increases neuronal activity in early visual areas in light as well as in darkness. This suggests that visual processing is influenced by locomotion independent of visual input. Combining mobile electroencephalography, motion- and eye-tracking, we investigated the influence of overground free walking on cortical alpha activity (~10Hz) and eye movements in healthy humans. Alpha activity has been considered a valuable marker of inhibition of sensory processing and shown to negatively correlate with neuronal firing rates. We found that walking led to a decrease in alpha activity over occipital cortex compared to standing. This

decrease was present during walking in darkness as well as during light. Importantly, eye movements could not explain the change in alpha activity. Nevertheless, we found that walking and eye related movements were linked. While the blink rate increased with increasing walking speed independent of light or darkness, saccade rate was only significantly linked to walking speed in the light. Pupil size, on the other hand, was larger during darkness than during light, but only showed a modulation by walking in darkness.

Analysing the effect of walking with respect to the stride cycle, we further found that blinks and saccades preferentially occurred during the double support phase of walking. Alpha power, as shown previously, was lower during the swing phase than during the double support phase. We however could exclude the possibility that the alpha modulation was introduced by a walking movement induced change in electrode impedance. Overall, our work indicates that the human visual system is influenced by the current locomotion state of the body. This influence affects eye movement pattern as well as neuronal activity in sensory areas and might form part of an implicit strategy to optimally extract sensory information during locomotion.

Keywords: Mobile EEG; alpha oscillations; blinks; saccades; locomotion

2.1 Introduction

Exciting findings from electrophysiological research in the animal model suggest that an increased walking speed results in enhanced neural activity in the visual domain. The firing rates of neurons in the primary visual cortex of mice, a cortical area responsible for processing basic visual input, are modulated depending on the running speed even in complete darkness (Ayaz, Saleem, Scholvinck, & Carandini, 2013; Clancy, Orsolic, & Mrsic-Flogel, 2019; Dadarlat & Stryker, 2017; Y. Fu et al., 2014; Keller, Bonhoeffer, & Hubener, 2012; Lee et al., 2014; Niell & Stryker, 2010; Polack, Friedman, & Golshani, 2013; Saleem, Ayaz, Jeffery, Harris, & Carandini, 2013). For review, please see (Busse et al., 2017; Händel & Scholvinck, 2019). This modulation goes beyond the influence of arousal (Vinck, Batista-Brito, Knoblich, & Cardin, 2015). Similar effects have been reported in invertebrates (Chiappe, Seelig, Reiser, & Jayaraman, 2010; Maimon, Straw, & Dickinson, 2010; Weir, Schnell, & Dickinson, 2014). While there is behavioural and electrophysiological work indicating that movements and cognitive processes such as memory, attention and perception are linked in humans (Bullock, Cecotti, & Giesbrecht, 2015; Bullock, Elliott, Serences, & Giesbrecht, 2017; Conradi et al., 2016; De Sanctis, Butler, Malcolm, & Foxe, 2014; De Vos, Gandras, & Debener, 2014; Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Kranczioch, Zich, Schierholz, & Sterr, 2014; Labonté-LeMoyne et al., 2015; Lin, Wang, Wei, & Jung, 2014; McMorris & Graydon, 2000; Schmidt-Kassow, Heinemann, Abel, & Kaiser, 2013; Wascher, Heppner, & Hoffmann, 2014), work showing an influence of locomotion on visual cortical activity as shown in animals is sparse in humans. In this respect, two recent studies showed that walking can lead to increased surround suppression (Benjamin, Wailes-Newson, Ma-Wyatt, Baker, & Wade, 2018) and peripheral visual information processing (Cao & Händel, 2019) in humans. Both studies provided evidence that locomotion can also lead to a change in visual processing of a stimulus, as has been shown in animals.

In human non-invasive electrophysiology, one possibility to look at ongoing activity is the power analysis of sustained oscillatory activity. Alpha activity, as a marker of inhibitory activity (Händel, Haarmeier, & Jensen, 2011; Klimesch, 1999; Klimesch, Sauseng, & Hanslmayr, 2007), has been found to be closely related to the firing rates of single neurons (Haegens, Nacher, Luna, Romo, & Jensen, 2011). A reduction in alpha power during walking

could therefore mark an increased activity in humans comparably to that found in animals. Indeed there have been previous reports of decreased oscillatory power in the alpha band (~10 Hz) during movements (e.g. walking) and navigation (Cao & Händel, 2019; Ehinger et al., 2014; Lin et al., 2014; Scanlon, Townsend, Cormier, Kuziek, & Mathewson, 2017). Additionally, there are reports of alpha and beta oscillatory power (mainly over sensorimotor cortex) being modulated by the phase of walking (see e.g. (Gwin, Gramann, Makeig, & Ferris, 2011; Roeder, Boonstra, Smith, & Kerr, 2018; Wagner, Solis-Escalante, Scherer, Neuper, & Müller-Putz, 2014). A typical finding is that alpha power is lower during the swing phase compared to the double support phase of walking. However, it is not clear if the phase modulation of brain oscillations during walking is contributed by an electrode impedance change. It is possible that a specific walking phase (e.g. the heel strike) may lead to a change of the electrode impedance due to a small turbulence introduced by the movement.

When participants are allowed to freely move without any restrictions, as in the current study, it is very important to keep in mind that movements influence each other. Body movements have been shown to interact on various scales. For example, if the head is free to move, an increased saccade rate can be found (Kowler, 1991). Whereas if the head is fixed, very small saccades referred to as microsaccades will increase in rate and/or amplitude (Collewijn & Kowler, 2008). Walking and eye-related movements also seem to be tightly linked. A recent study has shown a delicate coordination between gaze and gait cycle during natural overground walking (Matthis, Yates, & Hayhoe, 2018). Earlier work additionally suggests a temporal relationship between foot and eye movements by showing that saccades during walking are most likely made in the double support phase just before the toe-off (Hollands & Marple-Horvat, 2001).

In the current study, we ask if the alpha power decrease during walking is independent of visual input (e.g. in the dark) and thereby comparable to the animal findings. The walking phase modulation of alpha power is further investigated by measuring the electrode impedance during a full stride cycle. Additionally, the effect of walking and walking phase on eye movements (e.g. saccades) is investigated. This is an interesting question by itself but also contributes to the interpretation of the changed brain activity during walking as changed eye movements may also lead to a changed brain activity.

2.2 Materials and Methods

2.2.1 Participants

30 healthy participants (20 females; mean age: 29.2; SD: 8.0) were recruited from a local participant pool for the main experiment, and 18 healthy participants (10 females; mean age: 31.5; SD: 4.7) were recruited for the electrode impedance measurement during walking. All participants gave written informed consent prior to the study and received monetary compensation after the study. The study was approved by the local ethics committee (Department of Psychology, University Würzburg) and was conducted in accordance with the Declaration of Helsinki and the European data protection law (GDPR).

2.2.2 Task and procedure

In the speed condition, participants were standing still (speed = 0), slow walking (low speed) or normal walking (normal speed) (i.e. 3 levels; main experiment). Participants chose their own comfortable walking speed with the constraint that they should walk slower in the slow walking as compared to the normal walking. Participants were engaged with normal overground walking instead of treadmill walking as commonly seen in previous walking studies (e.g. (Lin et al., 2014). Each speed was conducted in two lighting levels: in the dark or in the light. Therefore, this is a 2 (lighting condition: light vs. dark) by 3 (speed condition: standing still, slowing walking, and normal walking) within-subjects design. Each of the 6 levels was tested in a 76.5-second session, and the order was randomised. Given the prominence of alpha activity in EEG data, a 76.5-second recording session should be more than enough to achieve a fair assessment of the activity strength. A one-second tone was delivered in the beginning and at the end of each session signalling the session start/end. There was a break of about 2 minutes between each session. A 3D-printed black plastic blindfold, consisting of a goggle like structure (fitted around eye tracking glasses, see below for details) with a front cover, together with an opaque canvas wrapped around the participant's head created a maximally dark environment. Only a few participants reported seeing very dim, constant beams in the created dark environment. In the light level, the front cover of the blindfold was removed. The average field of view measured from 2 participants in a pilot study was 110^{o} (horizontal) and 50^{o} (vertical). Participants were told to keep their

eyes open in all testing sessions. Prior to the current task, participants had completed another unrelated EEG study involving a visual detection task as described elsewhere (Cao & Händel, 2019). A controlled saccade test and some questionnaire data were collected after the task. The experiment was conducted in a large activity hall (about 30m x 50m; wooden floor) of the university gym. In all sessions in which walking was required, participants stayed within an area of about 100 m^2 in the centre of the activity hall. The experimenter was always present, quietly monitoring the walking path. A warning was given when participants walked too close to the wall. In total, 9 participants received on average 3 warnings when walking in the dark.

For the impedance measurement, another 18 participants were tested (different cohort from the main experiment). The task was similar to the normal walking session in the main experiment (in the light). Each participant was tested for 3 minutes in two separate testing sessions: one session with the electrode impedance measured throughout the 3-minute testing, and the other without. The testing was conducted in a smaller room (about 5m x 6m).

2.2.3 Data recording

EEG data were collected using a Smarting mobile EEG system (mBrainTrain LLC, Serbia), which has 24 recording channels with a sampling rate of 500 Hz. We used 6 channels for EOG (electrooculogram) recording (for each eye: one below and one above the eye, one to the outer canthus) and 18 channels for EEG recording (with 1 electrode on each earlobe for possible re-referencing; see Figure ***1c*** for EEG channel distribution). A common mode sense active electrode placed between Fz and Cz was used for online reference. The EEG signal amplifier and data transmitter are integrated into a little box (82 x 51 x 12 mm; 60 grams) which is attached to the back of the EEG cap. Data transmission is achieved via bluetooth. Motion data (velocity and acceleration; sampling rate: 120 Hz) were collected using a Perception Neuron system (https://neuronmocap.com/products/perception_neuron; Noitom Ltd, China). Three-dimension velocity and three-dimension acceleration data were collected from three sensors: one attached to each foot ankle (a few centimetres above the lateral malleolus) and the third one attached to the participant's back (at the waist level). The motion sensors were firmly attached on the top the participants' clothes. The pupil size was measured, only in the main experiment, with mobile eye-tracking glasses (SMI-ETG,

SensoMotoric Instruments GmbH, Germany), with a sampling rate of 120 Hz. The glasses were worn under the blindfold during the testing. Triggers for recording session start/end were generated with the software Lab Streaming Layer (https://github.com/sccn/labstreaminglayer), which was also used for collecting and synchronizing other streams of data (EEG, motion data and pupil size data). A Dell laptop (model: Latitude E7440) was used for running the experimental program. During the experiment, participants carried the laptop in a rucksack.

2.3 Data analysis

All the data analysis detailed below was completed using the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) and in-house scripts running on Matlab (The MathWorks Inc., USA).

2.3.1 Alpha power analysis

For each 76.5-second testing session, the EEG data were re-referenced to the grand average (excluding EOG channels and the 2 earlobe channels, i.e. 16 channels were used for analysis) before a low-pass filter at 100 Hz (a windowed sinc finite-impulse-response filter with Kaiser windowing was used for all the filtering processes unless otherwise stated) and a high-pass filter at 1 Hz were applied. The filtered data from 6 testing sessions were then combined into one data structure and reduced to 10 dimensions with principal component analysis, which was followed by an independent component analysis (ICA). The power spectrum of each ICA component was obtained using Welch's method (1 second time window, 50% overlap, 1 Hz resolution). ICA components were selected for further analysis if an alpha peak was found in the power spectrum and if the component topography has higher loading on occipital sensors than other sensor. Specifically, a component was selected if all the following requirements were met: 1. There were local peaks from 6 to 14 Hz in the component power spectrum; 2. The width of the local peak, which was defined as the frequency width between the two adjacent local minimums, should be at least 4 Hz (avoiding noisy transient peaks). If there were more than one local peak, the local peak with the largest width was taken (also for step 3); 3. The power at the local peak frequency should be at least 3 times higher than the mean power between 20 and 50 Hz (avoiding components with a

broad band high power); 4. In the ICA topography, the maximum absolute weight from sensors in the occipital area (O1, O2, and POz) was larger than the maximum absolute weight from all other sensors. Four participants were excluded as no components fulfilled the above requirements. On average, 2.4 components (SD: 0.8) were obtained from the remaining 26 participants. Each alpha component was partitioned back into the 6 testing sessions, and the average power spectrum of all components was calculated for each testing session. For alpha topography (Figure ***1c***), the selected components were projected back into sensor space and the alpha power was obtained for each sensor using Welch's method with the aforementioned parameters.

2.3.2 Eye movement-related analysis

Saccade detection

Saccade detection was based on the so-called REOG (radial EOG) component, which is the difference between the mean of all 6 EOG channels and the Pz channel. REOG component was band-pass filtered between 20 and 90 Hz using a 6th order Butterworth filter and then Hilbert transformed to obtain the amplitude envelop. All data points where the amplitude value deviated from the mean by 2.5 standard deviations were considered saccade-related and were grouped into one saccade if they were less than 20 ms apart. The above saccade detection procedure was performed separately for each testing session. This method was shown to be able to detect saccades very reliably when there are no head movements (Keren, Yuval-Greenberg, & Deouell, 2010). However, applying the same method to a free walking setting, one needs to keep in mind that the method actually detects a relative movement between the eyes and the head. When the eyes maintain fixation head movements may lead to an increase in the amplitude of REOG signal. The vestibulo-ocular reflex would be an example of such behaviour. We want to point out that during our experiment there was no constraint on head or eye movements. We assume that most eye movements were part of the normal orienting movements that combine head and eye movements in addition to small corrective movements. A classical vestibulo-ocular reflex as introduced by unexpected head movements or head rotation during forced fixation did not occur during our experiment. In supplementary Figure ***S1a***, the saccadic spike potentials of detected saccades were shown, which seem quite comparable to those detected during head fixation.

Blink detection

Blinks were detected from the vertical EOG component, i.e. the amplitude difference between the EOG channels above and below eyes. The vertical EOG component was high-pass filtered at 0.2 Hz and low-pass filtered at 10 Hz. A blink was marked if the vertical component crossed an individually defined threshold. The threshold was determined based on the amplitude of EOG component from individual data through visual inspection (the testing condition information was not available to the researcher during inspection) and the same threshold was used for all testing sessions of the same participant. The mean threshold across participants was 50.8 μV (SD: 11.8 μV). Blinks with the ratio between amplitude standard deviation and mean amplitude smaller than 0.2 were excluded. Adjacent blink points within 100 ms were combined into one blink. Results of blink detection from both eyes were quite similar. Only results from the left eye were used.

Pupil size

Raw pupil size (radius) data were quite noisy. For the complete pupil size data series (i.e. all the six testing sessions including the break time between sessions), missing data points were first excluded before a low pass filtering at 0.5 Hz was performed. Data from 2 participants were excluded as proportions of missing data points were more than 99%. The missing data points were then filled using a linear interpolation method (matlab 'fillmissing' function). The complete pupil size data were then grouped into each testing session and the average pupil size in each testing session was calculated (results were very similar between filled data and the data excluding missing points). For the remaining 28 participants, the 3 speed levels in the light had mean missing points of 6.7% (SD: 9.8%, standing still), 8.6% (SD: 11.2%, slow walking) and 9.2% (SD: 11.7%, normal walking), and in the dark had a mean of 15.3% (SD: 21.8%, standing still), 14.2% (SD: 17.4%, slow walking) and 18.8% (SD: 24.8%, normal walking). A 2 (lighting condition: light vs. dark) by 3 (speed condition: standing still, slow walking, and normal walking) within-subjects ANOVA (analysis of variance) comparing the proportion of missing data points gave only a significant main effect of lighting ($F(1,27) = 11.39$, $p < 0.001$). The pupil size from the left eye was used (right eye data were similar to the left eye and produced statistical results not qualitatively different from the left eye in all related tests).

2.3.3 Analysing the relationship between alpha power and eye-related movements

To analyse the possible relationship between alpha power and eye-related movements, alpha power in each 1 second epoch was obtained. The 76.5-second data in each session (i.e. the selected ICA components) were divided into epochs of 1-second with 0.5 second overlap between epochs (912 epochs in all testing sessions). The alpha power in each epoch was obtained using a fast Fourier transform after applying a Hamming window, which would give the same result of the mean alpha power in the whole 76.5 seconds as Welch's method did. Within each session, epochs with extreme alpha power were excluded using the MAD-median rule: let p be the alpha power in an epoch and P be the alpha power of all epochs within a testing session. If $|p - \text{median}(P)| \times 0.6745 > 2.24 \times$ MAD-median (the median absolute deviation from the median), this epoch is an outlier (Wilcox & Rousselet, 2018). The epochs were grouped depending on the number of saccades/blinks detected or the average pupil size. Epochs with more than 5 saccades (5.5% of all epochs) or more than 1 blink (9.2% of all epochs) were excluded. On average, there were 146.77 epochs (SD: 55.89) with 0 saccade, 239.46 epochs (SD: 40.65) with 1 saccade, 251.77 epochs (SD: 36.46) with 2 saccades, 163.12 epochs (SD: 48.58) with 3 saccades, and 64.73 epochs (SD: 22.40) with 4 saccades in all testing sessions. There were 472.08 epochs (SD: 172.68) with 0 blink, and 355.77 epochs (SD: 115.90) with 1 blink. For each participant, the pupil size data were divided into 5 groups from lowest pupil size to highest pupil size with equal number of epochs within each group. Alpha power was then compared between different groups separately for saccade rate, blink rate, and pupil size.

2.3.4 Walking phase and related analyses

The walking phase information was estimated from the velocity data (see also Figure ***3a*** for an illustration). Three-dimension velocity data were transformed to one-dimension speed data using the following formula: speed = sqrt((velocity_x)^2 + (velocity_y)^2 + (velocity_z)^2), where velocity_x, velocity_y, and velocity_z indicate the velocity data in three orthogonal dimensions. For each testing session, the speed time series from both ankles were added up and the combined speed time series was low-pass filtered at 2 Hz (walking speed data from 1 participant was missing due to technical error). Local minimum speed points were identified from the combined speed time series as the start point of a stride cycle (note that

the start point of a stride cycle was also the end point of the stride cycle before). The stride cycle, as obtained here, did not distinguish between left foot stride and right foot stride. In all related analysis, stride cycles (steps) with a particularly long duration (i.e. the duration between two consecutive local minimum speed points) were excluded using the MAD-median rule. The local maximum speed point between two local minimum speed points was also identified for plotting the average speed profile of stride cycles (Figure ***3b***). The average duration of stride cycles was 1.13 s (SD = 0.35 s) during slow walking in light, 0.62 s (SD = 0.08 s) during normal walking in light, 1.14 s (SD = 0.32 s) during slow walking in dark, and 0.66 s (SD = 0.10 s) during normal walking in dark. The average number of stride cycles was 68.4 (SD: 17.5) during slow walking in light, 120.6 (SD: 17.3) during normal walking in light, 65.5 (SD: 14.9) during slow walking in dark, and 108.4 (SD: 11.9) during normal walking in dark. For the analysis of possible modulatory effects from walking phase, the time period between two local minimum speed points (i.e. one stride cycle) was divided into 9 smaller equally spaced time periods, i.e. 9 walking phases. Since the walking phase was defined based on the continuous walking speed data, we refer to a phase as low speed phase when the walking speed reaches a local minimum (i.e. in both ends of a stride cycle) and a phase as high speed phase when the walking speed is high (i.e. in the middle of a stride cycle). The low speed phase may correspond to the canonically defined double support phase when both feet are touching the ground. The high speed phase (especially phase 5 in the middle) would correspond to the canonically defined swing phase with one foot in the air. The average alpha power, saccade rate, blink rate, and the average pupil size were computed for each walking phase. The alpha power evolution over time was also calculated for each testing session. This is necessary for the analysis of the relationship between alpha power and walking phase. Each alpha ICA component was band-pass filtered (Hamming window) between 8 and 12 Hz. A Hilbert transform was applied to the filtered data so that a power envelope can be obtained for each component before averaging. Note that the alpha power obtained in this way was much larger in amplitude as compared to the alpha power obtained using Welch's method. Steps that with extreme alpha power were excluded using the aforementioned MAD-median rule.

2.3.5 Electrode impedance

The continuous impedance data can be calculated from the signal power at 125 Hz for each electrode with the Smarting mobile EEG system when the impedance measurement was switched on. The power at 125 Hz was obtained for each sampling point using a 200 ms window after applying a Hamming tapper. The error in the measured impedance is about 1.5 kohm, so the impedance may appear slightly below 0 when the connection between the scalp and the electrode is very good. The impedance from 4 electrodes showing very strong alpha activities ('O1', 'O2', 'P7', 'P8') were averaged, and sorted into different walking phases before being compared (similar to the analysis of the relationship between walking phase and alpha power). Data from 2 participants were not included due to technical error during the recording, leaving 16 participants in the final results.

2.3.6 Statistical analyses

Within-subjects ANOVA, e.g. a 2 (lighting condition: light vs. dark) by 3 (speed condition: standing still, slow walking, and normal walking) within-subjects ANOVA comparing alpha power, and (two-tailed) paired t test were carried out for various comparisons detailed in the results section. Throughout the manuscript, all statistical comparisons were non-parametric, which was implemented through the randomisation test (parametric statistics gave similar results in each of test reported in the whole manuscript). In the randomisation test, the variables were randomly exchanged between conditions within each participant to obtain the distribution of the statistical variable (F value in ANOVA, mean difference between conditions in t test) under the null hypothesis, i.e. there are differences between conditions. The statistical variable obtained from the original data (no randomisation) was then compared to the null distribution to derive a *p* value. The within-subjects ANOVA algorithm was implemented by Gladwin (Gladwin, 2020), and the paired t test was implemented by ourselves. Statistical results are reported as significant when the *p* value is smaller than 0.05, and corrections for multiple comparisons were mentioned in the text whenever they were performed.

2.4 Results

2.4.1 Walking state modulates alpha power, eye-related movements, and pupil size

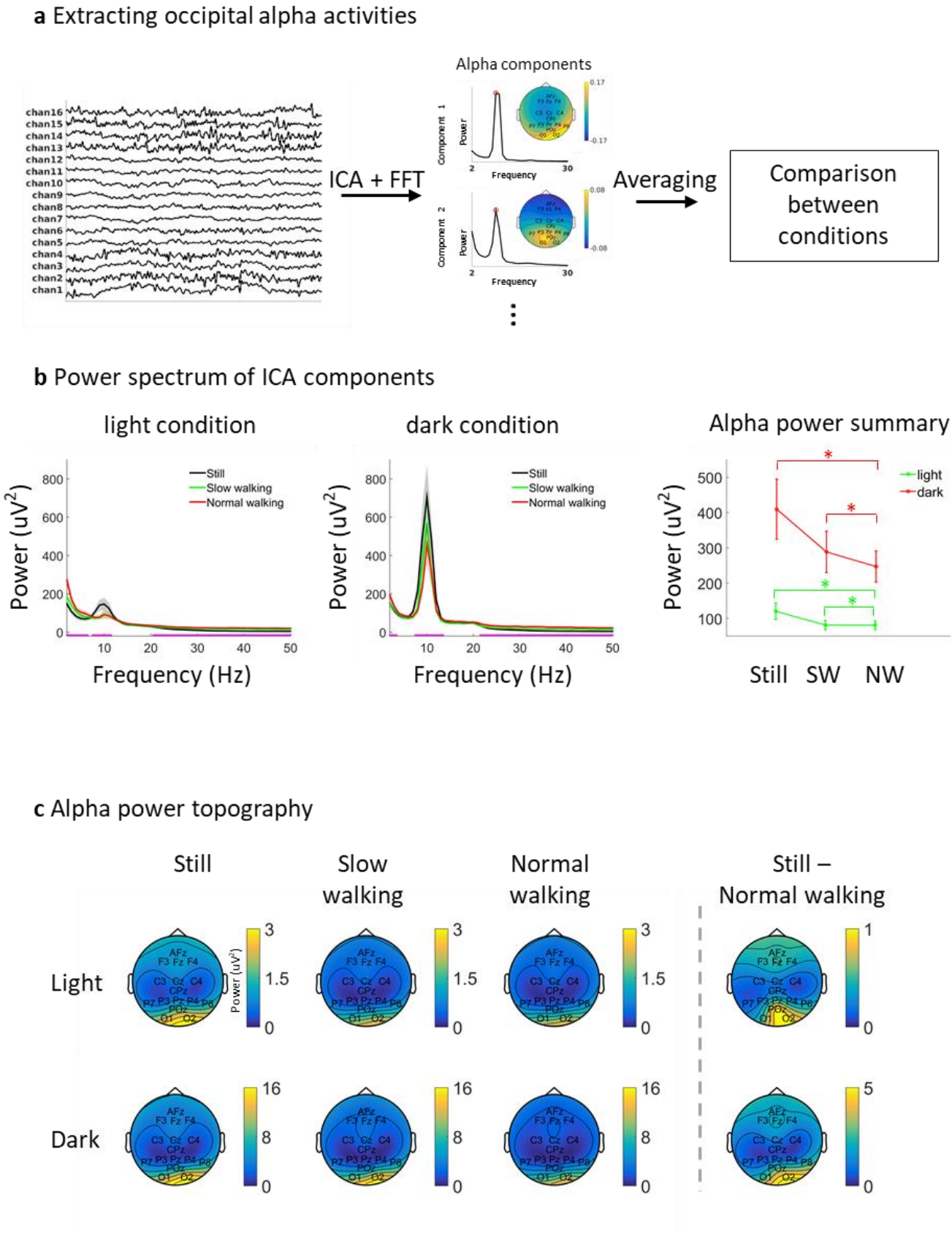


Figure 1. Alpha decreases during walking. (**a**) A schematic illustration of the EEG data analysis approach. Preprocessed data were subjected to independent component analysis and the ICA

components with high alpha power from the occipital area were identified automatically. The selected ICA components were then averaged within each testing session for further comparison. (**b**) EEG power spectra from alpha ICA components in each condition (left and middle). The magenta line on the abscissa marks the frequency bands showing significant differences between speed levels (FDR adjustment for multiple comparison) separately for the light and dark. One the right, the alpha power in each condition was plotting separately for better visualisation. Asterisks indicate $p < 0.05$. Shading and vertical lines indicate ±1 standard error. N = 26. (**c**) The topography of alpha power in each condition. The strongest activation (column 1 to 3) and the most prominent difference between standing still and normal walking (column 4) were found in the occipital area.

The average walking speed as detected by a motion sensor attached to the back was 0.53 m/s (SD: 0.18) during slow walking in light, 1.12 m/s (SD: 0.17) during normal walking in light, 0.50 m/s (SD: 0.17) during slow walking in dark, and 1.12 m/s (SD: 0.17) during normal walking in dark. A 2 (lighting condition: light vs. dark) by 2 (speed condition: slow vs. normal walking) within-subjects ANOVA indicated that participants walked significantly faster during normal walking than during slow walking ($F(1,28) = 243.34$, $p < 0.001$), and in light than in dark ($F(1,28) = 29.86$, $p < 0.001$). A significant interaction was also found ($F(1,28) = 16.48$, $p < 0.001$), which was due to the fact that there was no significant difference in speed during slow walking between light and dark ($t(28) = 1.65$, $p = 0.11$), but normal walking was significantly faster in light than in dark ($t(28) = 5.47$, $p < 0.001$).

ICA components with strong alpha activity (8-12 Hz) was extracted (Figure ***1a***). Unsurprisingly, alpha activities from the extracted ICA components were very strong (Figure ***1b***). A one-way within-subjects ANOVA was first carried out to compare the power spectra between speed levels for each frequency between 2 and 50 Hz, separately for the light and the dark lighting levles (multiple comparisons were adjusted with false discovery rate, FDR) (Yekutieli & Benjamini, 1999). Significant differences in the alpha band were found in both lighting levels. We then specifically compared alpha power using a 2 (lighting condition: light vs. dark) by 3 (speed condition: standing still, slow walking, and normal walking) within-subjects ANOVA. The results showed significant main effects of lighting ($F(1,25) = 16.84$, $p < 0.001$) and speed ($F(2,50) = 11.49$, $p < 0.001$). A significant interaction was also found ($F(2,50)$

= 5.70, $p < 0.001$). Alpha power was lower in the light (mean = 94.08; SD = 78.20) compared to the dark (mean = 315.05; SD = 309.42). In the light, alpha power was lower in both slow walking (mean = 81.07; SD = 67.18; t(25) = -2.44, $p = 0.01$) and normal walking (mean = 80.92; SD = 62.66; t(25) = -2.67, $p = 0.003$) compared to standing still (mean = 120.26; SD = 119.59), with no significant difference being found between slow walking and normal walking (t(25) = 0.03, $p = 0.99$). A similar pattern was found in the dark, with alpha power being lower in both slow walking (mean = 288.55; SD = 297.80; t(25) = -4.03, $p < 0.001$) and normal walking (mean = 246.94; SD = 225.05; t(25) = -3.13, $p < 0.001$) compared to standing still (mean = 409.67; SD = 432.69), and not significantly different between slow walking and normal walking (t(25) = 1.36, $p = 0.20$). The interaction effect indicates that the effect of alpha decrease during walking in the dark (within-subjects one-way ANOVA comparing between speed levels: F(2,50) = 9.45, $p < 0.001$) was stronger than in the light (within-subjects one-way ANOVA comparing between speed levels: F(2,50) = 6.08, $p = 0.004$). The topography of alpha power in each condition showed a strong activation in the occipital area (sensors O1 and O2), suggesting a visual origin of the alpha oscillations considered here (Figure. ***1c***). The strongest alpha power difference between standing still and normal walking (still – normal walking) was also found in occipital sensors.

The same 2 (lighting condition: light vs. dark) by 3 (speed condition: standing still, slow walking, and normal walking) within-subjects ANOVA was then performed to compare saccade rate, blink rate and pupil size. For saccade rate (see supplementary Figure ***S1a*** for the saccadic spike potential for detected saccades), both main effects of lighting (F(1,29) = 11.23, $p = 0.001$) and speed (F(2,58) = 40.18, $p < 0.001$) were significant, including a significant interaction effect (F(2,58) = 17.13, $p < 0.001$) (Figure ***2a***). Post-hoc analysis for the interaction effect showed that saccade rate increased with speed in the light (slow walking vs. standing still: (t(29) = 7.11, $p < 0.001$; normal walking vs. slow walking: (t(29) = 3.58, $p <0.001$)) but not in the dark (all comparisons between speed level pairs gave p values larger than 0.05). For blink rate, only the main effect of walking was significant (F(2,58) = 31.52, $p < 0.001$), indicating that blink rate increased with speed (slow walking vs. standing still: (t(29) = 3.75, $p < 0.001$; normal walking vs. slow walking: (t(29) = 7.42, $p < 0.001$) (Figure ***2b***). For pupil size, the main effect of lighting (F(1,27) = 228.50, $p < 0.001$) and the interaction effect (F(2,54) = 3.51, $p = 0.04$) were significant (Figure ***2c***). Post-hoc analysis for the interaction effect

indicates that, in the dark, pupil size increased from standing still to slow walking (t(27) = 2.40, p = 0.02) and to normal walking (t(27) = 2.22, p = 0.03), with no difference being found between normal and slow walking (t(27) = 0.42, p = 0.69). Whereas in the light, no differences could be found between any speed level pairs (all p values were greater than 0.27).

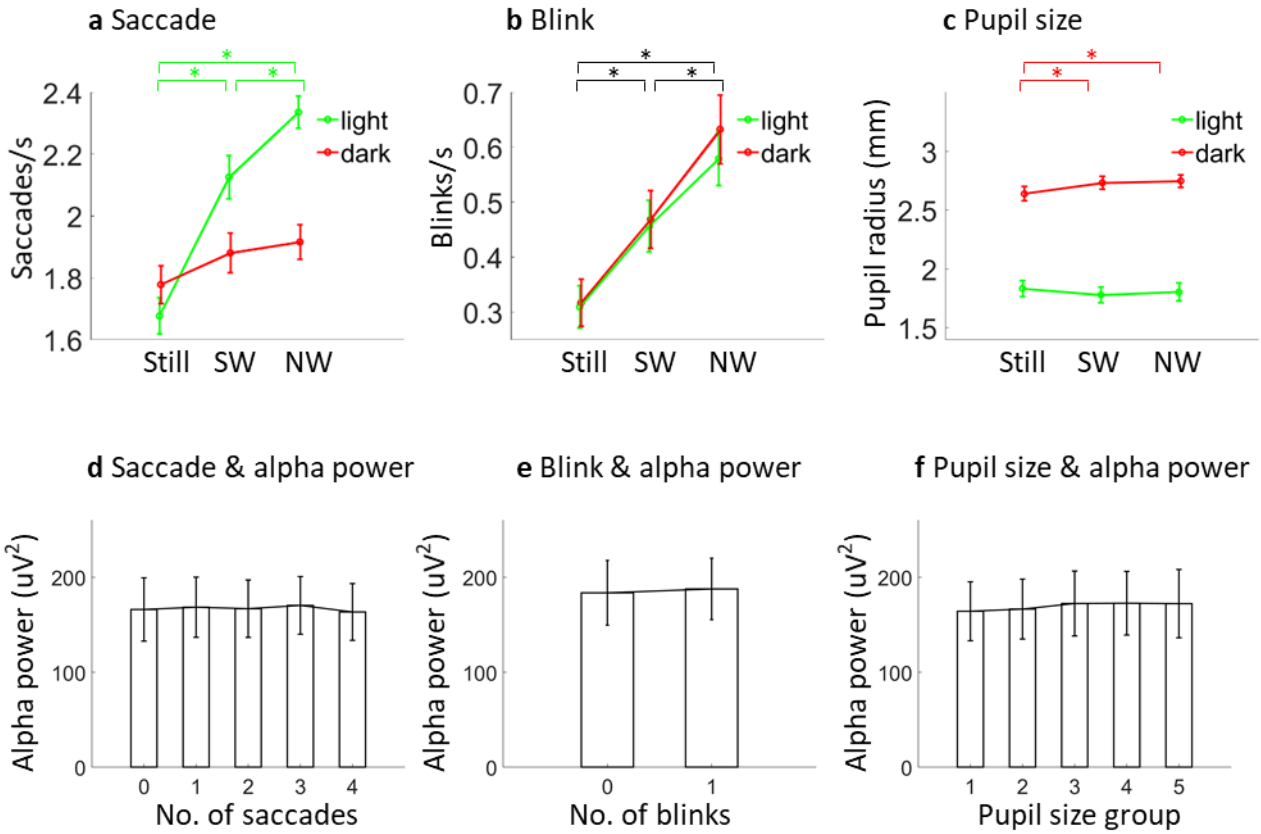


Figure 2. Eye-related movements, pupil size and alpha power. Saccade rate (**a**; N = 30), blink rate (b; N = 30) and pupil size (**c**; N = 28) depicted separately for each condition. Asterisks indicate p < 0.05. Black lines in (b) indicate comparisons in both light and dark. Alpha power was not modulated by the number of saccades (**d**; N = 26), blinks (**e**; N = 26), or the average pupil size (**f**; N = 24). In f, the pupil size increased from group 1 to group 5. Vertical lines indicate ±1 standard error. SW: slow walking; NW: normal walking.

2.4.2 No general link between alpha power and eye-related movements

Since walking modulates both alpha power and eye movements, it is important to ask if alpha power and eye-related movements are related in the current dataset. To test this, the 76.5-second data in each testing session were divided into epochs of 1-second with 0.5

second overlap between epochs. For each epoch, alpha power, numbers of saccades and blinks, and the average pupil size were obtained. Alpha power was not modulated by the number of saccades ($F(4,100) = 0.97$, $p = 0.44$) or blinks ($F(1,25) = 0.001$, $p = 0.98$) for data collapsed over all testing sessions (Figure ***2d-e***). Pupil size data were sorted into 5 groups from smallest pupil size to largest pupil size. Again, alpha power was not found to be different between groups ($F(4,92) = 0.72$, $p = 0.68$; Figure ***2f***).

2.4.3 Walking phase modulates alpha power

The walking phase was obtained based on the speed information from both ankles. Speeds from both ankles were added up and the local minimum speed point was detected as the start and the end point of a stride cycle (Figure ***3a-b***). Each stride cycle was then divided into 9 equally long successive time periods, equivalent to 9 walking phases, with the first and the last phase (low speed phase) roughly corresponding to the double support phase and the middle phase (high speed phase) corresponding to the swing phase. The average alpha power within each phase was computed. Any modulatory effect from walking phase should lead to different strength of alpha power in different phases, which was tested with a 2 (lighting condition: light vs. dark) by 2 (walking speed condition: slow vs. normal walking) by 9 (walking phase) within-subjects ANOVA.

Significant main effects were found for lighting ($F(1,24) = 13.87$, $p < 0.001$) and walking phase ($F(8,192) = 6.68$, $p = 0.004$). The effect of lighting showed that alpha power was higher in the dark than in the light, which has been shown in the previous section. The effect of walking phase indicated that alpha power was lower in the low speed phase as compared to the high speed phase during a stride cycle (Figure ***3c***). No other effects from the three-way ANOVA were significant.

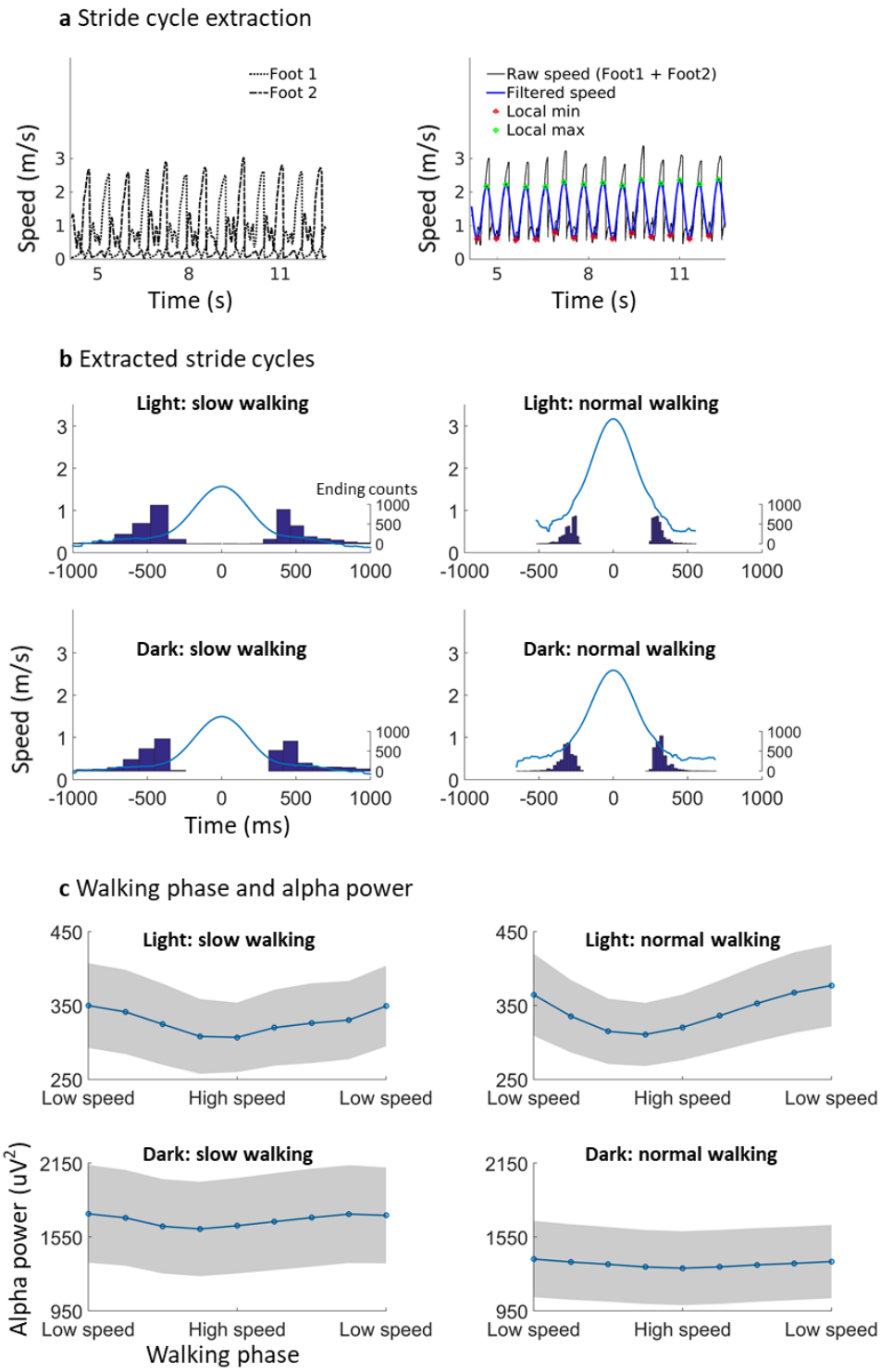


Figure 3. Walking phase modulates alpha power. (**a**) Illustration of stride cycle extraction. The walking speed from both ankles (left) were added up, and the combined raw walking speed time series data were filtered (right). The local minimum point and the local maximum point in the filtered data could then be found using the phase information. The local minimum point was used as the start/end point of a stride cycle. A subset of speed data during normal walking

in the dark from one participant was used for the illustration. (**b**) The extracted stride cycles from all participants (N= 29) in each condition. The walking speed of each stride cycle was aligned to the local maximum point (as shown in A), which is time point 0 on the x-axis, for calculating the average speed profile (blue line). The distribution of the duration between the local minimum point and the local maximum point is shown with histograms, with scales shown on the right of each plot. (**c**) Alpha power in different walking phases. Each stride cycle (from a local minimum to the next local minimum) was divided into 9 equal time windows. The low speed phase and high speed phase may roughly correspond to the canonically defined double support phase and swing phase, respectively. A clear modulation of alpha power by walking phase can be found. Shading indicates ±1 standard error. N = 25. (**c**) The electrode impedance was not modulated by the walking phase. The solid line shows the average impedance of all 16 participants, and the dashed line shows individual data (shading indicates ±1 standard error of measurements across all stride cycles). Note that negative impedance as due to the measurement error and indicated very good connection between the scalp and the electrode.

2.4.4 Walking phase does not modulate electrode impedance

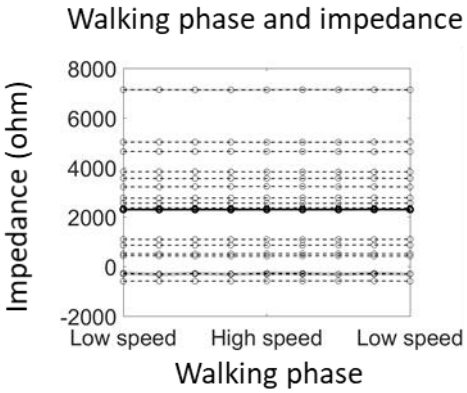


Figure 4. Walking phase does not modulate electrode impedance. The solid line shows the average impedance of all 16 participants, and the dashed line shows individual data (shading indicates ±1 standard error of measurements across all stride cycles). Note that negative impedance was due to the measurement error and indicated very good connection between the scalp and the electrode.

The electrode impedance was measured during normal walking with an additional 16 participants to test the possibility that the alpha power modulation by the walking phase, as reported in the last section, is due to an impedance change resulting from walking movements. However, the average impedance of 4 occipital sensors was not modulated by the walking phase ($F(8,120) = 0.71$, $p = 0.80$; Figure ***4***). Importantly, a significant alpha power modulation by the walking phase could still be detected from the 4 sensors ($F(8,120) = 4.72$, $p = 0.01$; supplementary Figure ***S2***).

2.4.5 Walking phase modulates eye movements

For saccade rate, significant main effects from the ANOVA were found for lighting ($F(1,28) = 27.37$, $p < 0.001$), walking speed ($F(1,28) = 7.72$, $p = 0.01$), and walking phase ($F(8,224) = 2.39$, $p = 0.02$) (Figure ***5a***). The effects of lighting and walking conform to previous results showing that saccade rates increase from dark to light, and from slow walking to normal walking. The effect of walking phase indicated that the saccade rate was different across walking phases. Furthermore, a significant interaction effect was found between walking speed and walking phase ($F(8,224) = 2.76$, $p = 0.02$). Post-hoc analysis indicated that the saccade rate was modulated by walking phase during normal walking ($F(8,224) = 3.40$, $p = 0.004$; one-way within-subjects ANOVA), but not during slow walking $F(8,224) = 0.97$, $p = 0.45$; one-way within-subjects ANOVA. During normal walking, the saccade rate appeared to be lower during the high speed phase than during the low speed phase. No other effects from the three-way ANOVA were significant.

For blink rate, a similar walking phase modulation effect was observed. Significant main effects from the ANOVA were found for walking speed ($F(1,28) = 37.38$, $p < 0.001$) and walking phase ($F(8,224) = 2.68$, $p = 0.02$) (Figure ***5b***). The effect of walking speed showed that the blink rate increased with walking speed, as already showed in the previous analysis. The effect of walking phase indicated that the blink rate was different across walking phases. A significant interaction effect was also found between walking speed and walking phase ($F(8,224) = 3.52$, $p = 0.01$). Similar to the pattern showed by the saccade rate, post-hoc analysis indicated that the blink rate was modulated by walking phase during normal walking ($F(8,224) = 3.71$, $p = 0.004$; one-way within-subjects ANOVA), but not during slow walking ($F(8,224) = 1.81$, $p = 0.09$; one-way within-subjects ANOVA). During normal walking, the blink

rate appeared to be lower during the high speed phase than during the low speed phase. No other effects from the three-way ANOVA were significant.

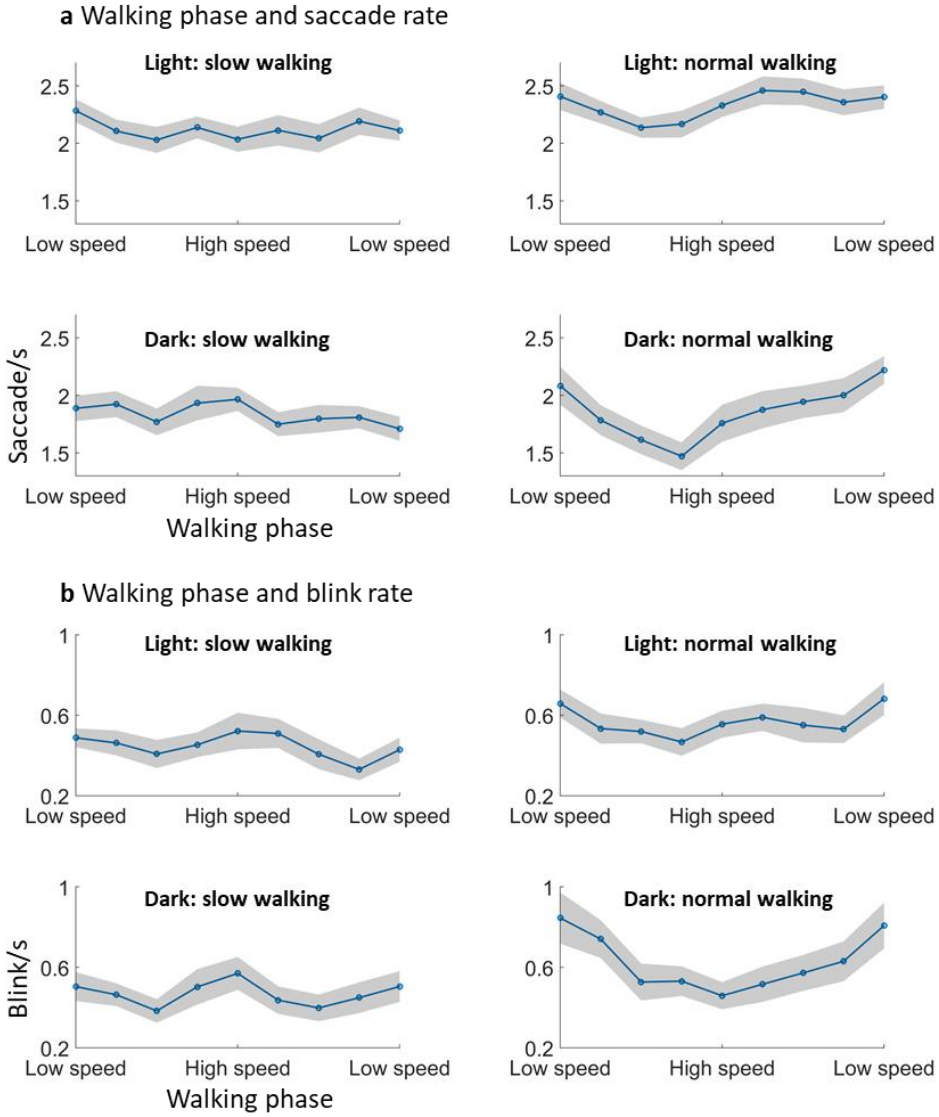


Figure 5. Walking phase modulates saccade and blink rate. (**a**) The saccade rate was lower in the high speed phase as compared to the low speed phase, which was only found in normal walking. (**b**) A similar modulation during normal walking was found with the blink rate, i.e. participants showed less blinks in the swing phase of walking. Shading indicates ±1 standard error. N = 29.

For pupil size, only a main effect of light was significant ($F(1,26) = 200.32$, $p < 0.001$) from the ANOVA, which indicated that the pupil size was smaller in the light than in the dark. See supplementary Figure ***S3*** for the pattern of pupil size across walking phases.

2.5 Discussion

With the study at hand, we show that natural walking leads to lower occipital alpha power as well as an increased saccade and blink rate and a larger pupil size. The modulation of alpha power and blink rate by walking was observed when participants were walking in light as well as in dark, suggesting that the visual input during walking is not the driving factor. Walking phase was further found to modulate alpha power, and blink and saccade rate in both light and dark. We discuss these findings below in detail.

Alpha power decrease due to walking (walking state modulation)

In both light and dark, alpha power considerably decreased during walking. Previous studies have reported such a modulation of alpha power by walking (Cao & Händel, 2019; Ehinger et al., 2014; Gwin et al., 2011; Lin et al., 2014; Scanlon et al., 2017). However, our results add important insights to this finding that help us to understand this prominent alpha modulation due to walking.

First, our results clearly indicated that alpha reduction during walking can be observed with a focus over occipital sensors, most likely reflecting a change of neural activity in the visual cortex. Previous studies on the alpha (or mu) modulation during walking focused on sensorimotor processing (García-Cossio et al., 2015; Gwin et al., 2011; Lin et al., 2014; Scanlon et al., 2017; Severens, Nienhuis, Desain, & Duysens, 2012; Storzer et al., 2016). The current study provided a strong support for the existence of a similar modulation effect of walking on visual cortical activity in humans to the effect as demonstrated through single cell recordings in animals. A reduction in alpha activity during walking in humans, which would imply a disinhibition of cortical activity, is consistent with the finding of increased firing rates in the visual cortex of mice during locomotion (e.g. (Saleem et al., 2013). Please find below a discussion on the validity of our alpha results with respect to localisation. Second, we showed that the modulation of alpha power due to walking is independent of the visual input. In the dark, participants reported absolute darkness except a few participants, who reported a very faint and vague sensation of light, which entered through the connecting area between the shutter and the eye tracker. Third, our finding demonstrated such an effect in a task-free natural walking setting. This indicates that the necessity to focus on a specific task is not

relevant to the alpha power modulation by walking. Fourth, we showed that saccades, blinks, and pupil size could not explain the alpha power modulation by walking. It should be noted that the data analysis in this part (Figure ***2d-f***) was not tailored for a proper investigation of the relationship between alpha power and eye movements/pupil size. Therefore, a lack of relationship does not necessarily mean no relationship (e.g. see alpha lateralisation in the process of making a saccade (Belyusar et al., 2013). Rather, the results only indicate that the observed alpha power decrease during walking cannot be explained by changes in eye movements or pupil size during walking. Fifth, evaluating the change in signal to noise ratio, we saw an overall power increase in high and low frequencies during walking as compared to standing (Figure ***1b***; significant differences were indicated by the magenta line). However, the alpha modulation consisted of a decrease in the frequency limited alpha band. This is a clear indication, that the alpha change is not introduced by a walking induced change in noise. By additionally excluding order effects through an order randomisation of all testing sessions, our finding therefore suggests a specific link between alpha power and walking.

What could be the functional reason for such a decrease in alpha power during walking compared to standing still? Previous studies have identified a sensorimotor mu/beta suppression during walking as compared to standing (Wagner et al., 2012; Wagner et al., 2014). The modulated alpha activity during walking, as shown in the current study, was specifically picked up from the visual brain area (Figure ***1c***). In general, alpha activity, found in sensory areas, is often associated with attentional processes. Attending to a particular location or time point has been shown to lower the occipital alpha power which was further correlated with the improvement of visual perception (van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). Alpha power over visual cortex further reliably indicates the spatial focus of covert visual attention showing an increase in power for the unattended input (K. M. Fu et al., 2001; Kelly, Lalor, Reilly, & Foxe, 2006; Sauseng et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000; Yamagishi et al., 2003). The preferred interpretation of alpha power picked up over sensory areas is therefore inhibition of sensory input processing (Händel et al., 2011; Klimesch, 1999; Klimesch et al., 2007). A functional interpretation of the observed decrease in alpha power during walking could therefore be linked to a change in the attentional state while walking. A recent study presented behavioural and neurophysiological evidence that walking shifts preferred visual processing

towards the peripheral visual field (Cao & Händel, 2019). An overall reduction in alpha power during walking compared to standing still could therefore depict the reduced inhibition of the peripheral input.

Interestingly, alpha power decrease could be associated with an increase in neuronal activity investigating somatosensory areas in the monkey (Haegens et al., 2011). Interpreting our walking induced alpha power decrease in the light of the likely associated increase of neuronal activity, we believe that our findings are very well in line with recent animal work showing that activity in early visual cortex is increased by walking speed in complete darkness (Dipoppa et al., 2018; Erisken et al., 2014; Keller et al., 2012; Saleem et al., 2013). The significantly reduced alpha power in the light compared to the dark was further consistent with the idea that the alpha power analysed in the current work indexed the neural processing of visual input (see also (Ben-Simon et al., 2013; Cram, Kohlenberg, & Singer, 1977). Taken together, these exciting findings point to a general, species-unspecific modulation of perceptual mechanisms due to movement.

Walking state modulates eye-related movements and pupil size

In addition to changes in neuronal oscillatory power, walking had differential effects on eye related movements depending on the lighting level. The saccade rate increased with speed in the light but not in the dark. This is consistent with the idea of feedforward control of walking with visual information (Hollands & Marple-Horvat, 2001; Matthis, Barton, & Fajen, 2017). The increased saccade rate during walking in the light coincides with the increased processing demand of fast changing visual information to assist walking. No such processing demands of new visual information are required in the dark as no information is available. This might explain why the saccade rate did not increase when participants walked in the dark. Interestingly, the blink rate was also increased with speed. Visually demanding tasks, like a search task, are usually associated with a significantly decreased blink rate (Bauer, Strock, Goldstein, Stern, & Walrath, 1985; Cho, Sheng, Chan, Lee, & Tam, 2000). The finding, that the blink rate is equally affected by walking during darkness and light, further indicates that the modulation of blinking due to walking is independent of the visual input. We therefore assume that the increase in blink rate might be of the same nature as the link between blinking and speaking (Cruz, Garcia, Pinto, & Cechetti, 2011; von Cramon & Schuri,

1980) or blinking and button pressing (Cong, Sharikadze, Staude, Deubel, & Wolf, 2010; van Dam & van Ee, 2005) and rather based on a motor related interaction.

Pupil size increased while walking compared to standing in the dark, conforming to previous reports in mice (Erisken et al., 2014; Vinck et al., 2015). In the light, pupil size was expected to be modulated similarly (Benjamin et al., 2018), but for our data it showed no difference between speed levels in light. We suspect that a modulation could have been masked by changing luminance in the light. The testing room was non-uniformly lit (one side of the room was a bit brighter) which led to a change in luminance due to walking within this room. This would lead to an increase in variance of the measured pupil size, thereby masking moderate changes due to speed (supplementary Figure ***S1b***). Future studies on the pupil size during free walking should take the lighting condition into account. In the dark, the influence of luminance was absent.

Walking phase related modulation of alpha power

A walking phase related modulation in alpha power was found. Previous studies have shown a walking phase dependent power modulation in theta, alpha, beta, and gamma bands in a wide brain network including, posterior parietal, sensorimotor, and premotor areas (Artoni et al., 2017; Bradford, Lukos, & Ferris, 2016; Chéron et al., 2012; Gwin et al., 2011; Oliveira, Schlink, Hairston, Konig, & Ferris, 2017; Seeber, Scherer, Wagner, Solis-Escalante, & Müller-Putz, 2014, 2015; Severens et al., 2012). The observation of walking phase dependent alpha power modulation in the current study is consistent with those reports. However, we note that the walking phase modulation of alpha power should be interpreted cautiously, as the level of artefacts in the EEG signal may be different in different walking phases. There are competing accounts with regards to the level of artefacts in the EEG signal during walking (Castermans, Duvinage, Cheron, & Dutoit, 2014; Nathan & Contreras-Vidal, 2015; Snyder, Kline, Huang, & Ferris, 2015), but it is feasible that the double support phase may have more artefacts as the heel-strike (foot landing on the ground) is in this phase (e.g. see an example of EEG noise assessment during walking from (Bradford et al., 2016)). Our findings give further evidence that the observed alpha power modulation is unlikely due to artefacts since the electrode impedance did not change over the stride cycle (Figure ***4***). In fact, the difference in impedance between different walking phases was so small (less than 100 ohm) that it cannot

lead to any difference in the amplitude of measured signal (Ferree, Luu, Russell, & Tucker, 2001).

Walking phase modulates eye movements

The result of walking phase dependent eye movements corroborates such a non-visual link for blinks and it additionally suggests that also saccades are not exclusively influenced by visual input. For saccades, a preference for the double support phase (just before the toe-off) has been reported previously while visual input was present (Hollands & Marple-Horvat, 2001). We show that besides the saccade rate, the blink rate was also modulated by the walking phase and that both rates increased during the double support phase compared to the swing phase. It is important to note that the walking related artefact cannot explain the pattern of saccade rate as modulated by the walking phase (saccades were detected based on the spectral power between 20 and 90 Hz from the REOG component). A 2 (lighting condition: light vs. dark) by 2 (walking speed condition: slow vs. normal walking) by 9 (walking phase) within-subjects ANOVA testing the amplitude of the saccadic spike potential did not give a significant effect of walking phase ($F(8,224) = 0.87$, $p = 0.53$) (Supplementary Figure ***S1c***).

Considering the rhythmic nature of human bipedal walking, there could be a critical phase during which the execution of saccadic eye-movements is least disturbing for information acquisition. Due to saccadic inhibition, information processing is greatly reduced during the time of a saccade (Matin, 1974). During a blink, visual input is shut down due to eye lid closure as well as due to blink suppression (Volkmann, Riggs, & Moore, 1980). Since the double support phase, which includes heel-strikes, is also the moment when the visual system is most unstable due to the whole-body vibration imposed by heel-strikes, information acquisition might be suboptimal during this time point. Thus, a good strategy might be to make a blink/saccade during this double support phase so that it can be avoided in the swing phase when the visual system is relatively stable. Interestingly, the coupling between walking phase and preferred saccade as well as blink occurrence was also present in the dark. This makes the phase modulation effect specifically intriguing. Saccades and blinks do not have any effect on visual information in the dark. Nevertheless, they were still modulated by walking phase similarly to and even possibly slightly stronger than in the light. One possible

explanation is that the preference of saccade occurrence during walking phase, once introduced by visual feedback, is now hard-coded and independent of vision. Therefore, it might be the case that the walking phase modulation effect on saccades and blinks is controlled by a low-level neural circuit and much easier to be observed in the dark compared to light, in which case the visual input from the environment may have an additional influence on saccades and blinks.

The reason why the phase modulation effects for eye related movements in normal walking but not in slow walking is not clear. One possibility might be that deliberate walking (i.e. slow walking) requires more cognitive control, which might weaken a low-level link between walking phase and eye-movements. The other possibility might be that the power of the current study is too low to detect such a walking phase modulation during slow walking. A stride cycle during slow walking (~1.1 s) took about two times longer than a stride cycle during normal walking (~0.6 s). Therefore, the number of steps cycles available for analysis was much lower during slow walking as compared to normal walking in a 76.5-second testing window. Although we tend to assume that 70 steps cycles should be enough to capture a walking phase modulation effect during slow walking (if there is one), further studies should explicitly test this possibility by extending the testing time.

Limitations of the current study

Mobile EEG during unrestricted free walking always poses extra challenges due to its deviation from controlled stationary lab routines. We discuss these problems throughout the manuscript but want to shortly summarise and partly extend our considerations concerning artefacts and experimental limitations. In short, our main finding regarding the alpha power reduction due to walking was a frequency-band limited effect clearly excluding the problem of changed signal to noise ratio due to walking. Additionally, we controlled for eye movements, which are different between walking and standing still and pose a source of artefacts. We further measured impedance changes during walking with no indication that impedance changes could explain our findings.

Another challenge for mobile EEG is the reduced number of sensors which is necessary especially if subjects are freely walking instead of moving on a treadmill or a stationary bike.

Our number of 24 sensors, including 6 sensors for EOG, certainly does not permit a further analysis in source space. Nevertheless, as investigated in detail in a study by Lau and colleagues (Lau, Gwin, & Ferris, 2012), the number of sensors necessary for recording predominant electro-cortical sources is not large. Indeed, particularly for occipital or temporal activity, their results suggest that the pattern do not exhibit large changes by reducing the sensor number from 125 to 25 (see Figure 4 (Lau et al., 2012)). Therefore, staying in sensor space, ICA as applied by us is able to mark hotspots of activation, and the low number of sensors does not introduce a distortion but only results in a reduced spatial resolution. In our approach, we further picked those sources with a dominance over occipital area for further analysis. Importantly, it could have been feasible that even though we picked a focus over occipital sites, the difference between speed levels was introduced by changes with an only marginally overlapping spatial distribution. However, our Fig 1C (still – normal walking) clearly suggests that for the chosen components also the difference between speed levels was maximal at the power maximum. If the difference between speed levels was introduced by other sites, the difference should show a different distribution. Therefore, while the used number of sensor was suboptimal, our analysis and results nevertheless can demonstrate a change in power happening over occipital sites.

The walking phase was estimated from the combined walking speed data collected from both ankles. While the low speed phase and high speed phase of a stride cycle can be obtained accurately, the exact moment of heel-strikes and toe-offs cannot be determined. Furthermore, the left foot stride and the right foot stride were not distinguished in the current study. Despite these differences from a canonical gait phase analysis (see e.g. (Gwin et al., 2011)), our results are consistent with previous findings with regards to the walking phase modulation of alpha power (Artoni et al., 2017; Bradford et al., 2016; Chéron et al., 2012; Gwin et al., 2011; Oliveira et al., 2017; Seeber et al., 2014, 2015; Severens et al., 2012). Therefore, the current results are very likely replicable with a canonical gait phase analysis.

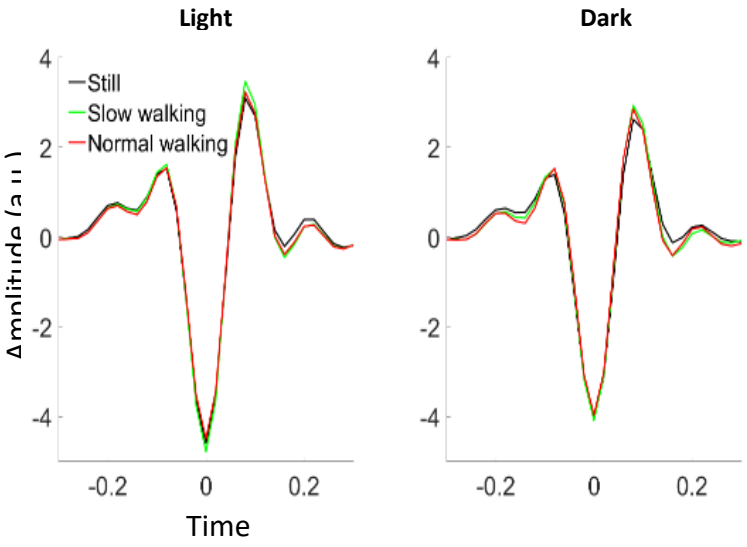
2.6 Conclusion

Our work indicates that the basis of visual perception, including neuronal processes and eye related movements, is influenced not only by the current demands of the visual input but also by the current movement state of the body. The above mentioned interactions

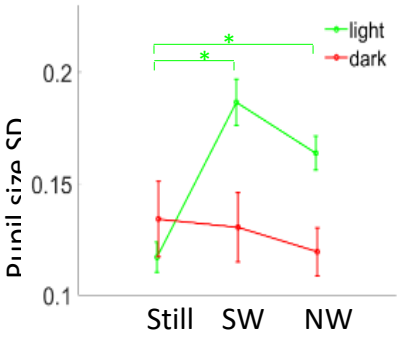
between eye and other body movements as well as the modulation of neuronal activity due to body movements suggest a large-scale process to optimize perception during natural behaviour. These findings highlight the importance of investigating perceptual processes in natural settings and considering body movements and their interactions when analysing perception.

2.7 Supplementary material (Study 1)

a Saccadic spike potentials



b Pupil size standard deviation



c Amplitude of saccadic spike potential across

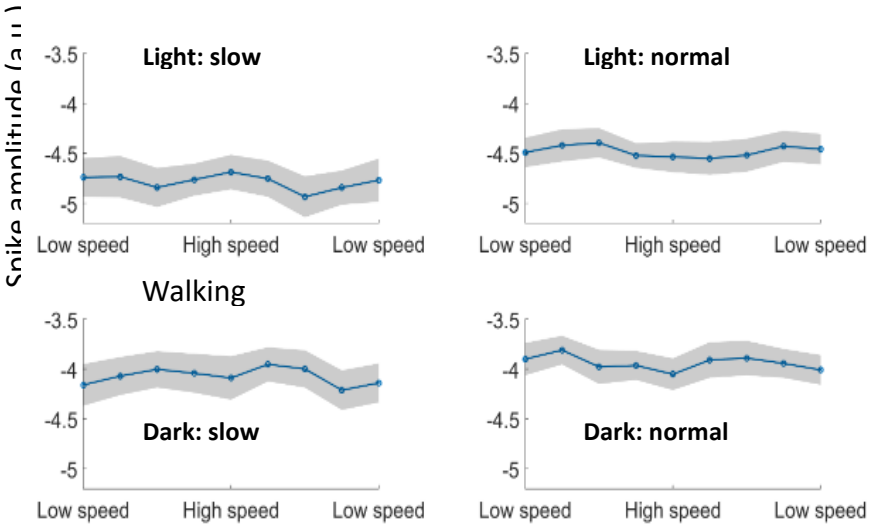


Figure S1. Saccadic spike potentials and pupil size variance. (**a**) Group average saccadic spike potentials in each testing session. For each participant, each detected saccade was aligned to the lowest amplitude point (time 0) and referenced to the mean amplitude of the Hilbert transformed REOG signal within each testing session through division. Clear saccadic spike potentials indicate reliable detection of saccades. See methods section for details of the saccade detection method. (**b**) The standard deviation of pupil size in each condition. A 2 (lighting condition: light vs. dark) by 3 (speed condition: standing still, slow walking, and normal walking) within-subjects ANOVA led to significant main effects of lighting ($F(1,27) = 4.66$, $p = 0.04$) and speed ($F(2,54) = 6.05$, $p = 0.007$), as well as a significant interaction effect ($F(2,54) = 7.89$, $p < 0.001$). Post-hoc analysis showed that the pupil size standard deviation was higher during walking than during standing in the light (slow walking vs. standing still: ($t(27) = 7.64$, $p < 0.001$; normal walking vs. standing still: ($t(27) = 4.53$, $p < 0.001$; normal walking vs. slow walking: ($t(27) = -1.96$, $p = 0.07$), whereas no such difference was found in the dark (all ps > 0.39). Asterisks indicate $p < 0.05$. Vertical lines indicate ±1 standard error. N = 28. SW: slow walking; NW: normal walking. (**c**) Walking phase does not modulate the amplitude of saccadic spike potentials. For each detected saccade, the amplitude of saccadic spike potential was taken at the time point of 0. A 2 (lighting condition: light vs. dark) by 2 (walking speed condition: slow vs. normal walking) by 9 (walking phase) within-subjects ANOVA was performed to test the amplitude. Significant main effects were found for lighting ($F(1,28) = 39.26$, $p < 0.001$) and walking speed ($F(1,28) = 8.50$, $p = 0.01$). Note that the threshold for saccade detection was determined separately for each testing session. Therefore, the amplitude difference between testing sessions would not contribute to the difference in the number of saccades deteted between sessions. No other effects for the ANOVA were significant. Shading indicates ±1 standard error. N = 29.

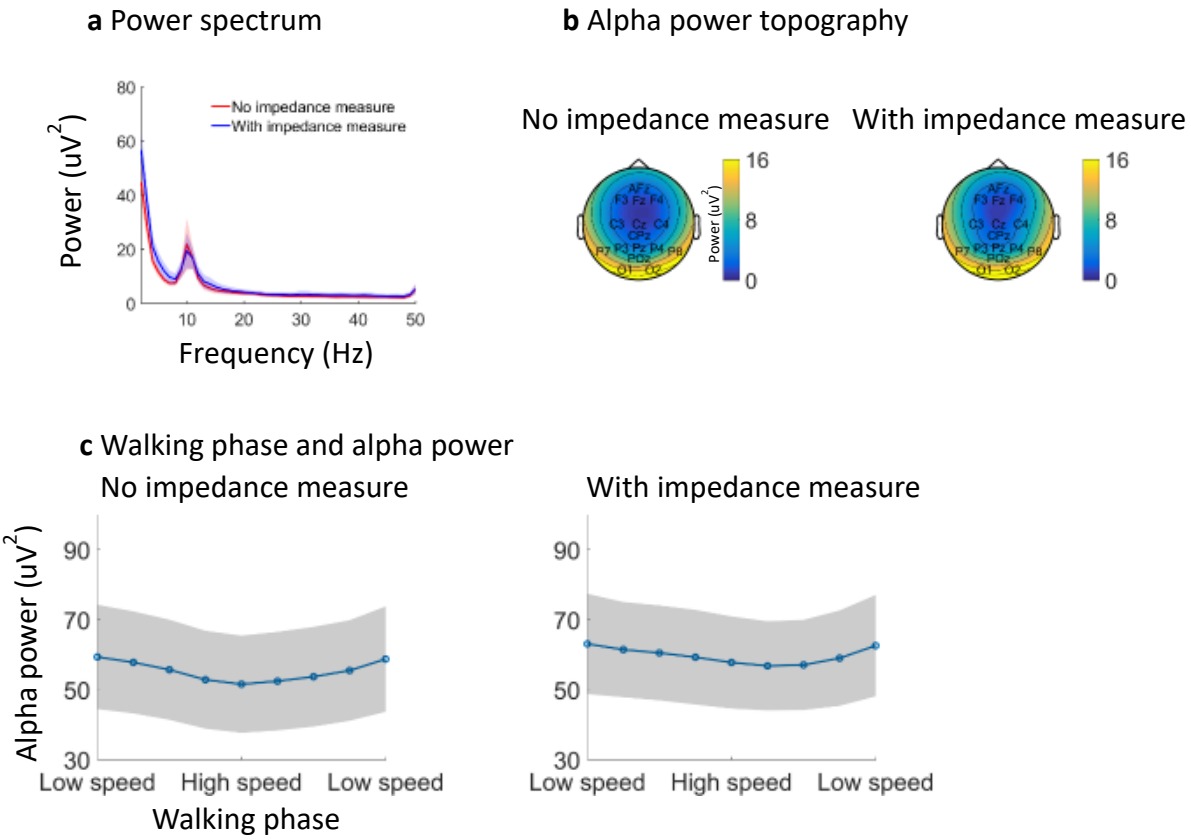


Figure S2. Impedance measure dataset. (**a**) The average EEG power spectra from four electrodes ('O1', 'O2', 'P7', 'P8'), with the impedance measure switched on or switched off. No significant influence was found on the power spectrum from the impedance measure. Shading indicates ±1 standard error. N = 18. (**b**) The topography of alpha power. (**c**) Alpha power in different walking phases. The alpha power was averaged over the four electrodes whose power spectra were plotted in (**a**). A 2 (impedance measure: no vs. yes) by 9 (walking phase) within-subjects ANOVA showed a significant main effect of walking phase ($F(8,120) = 4.72$, $p = 0.01$), which is similar to the results obtained with ICA components (Fig. 3B in the main text). No other effects were significant (impedance measure: $F(1,15) = 0.17$, $p = 0.66$; interaction: $F(8,120) = 0.91$, $p = 0.49$). Shading indicates ±1 standard error. N = 16.

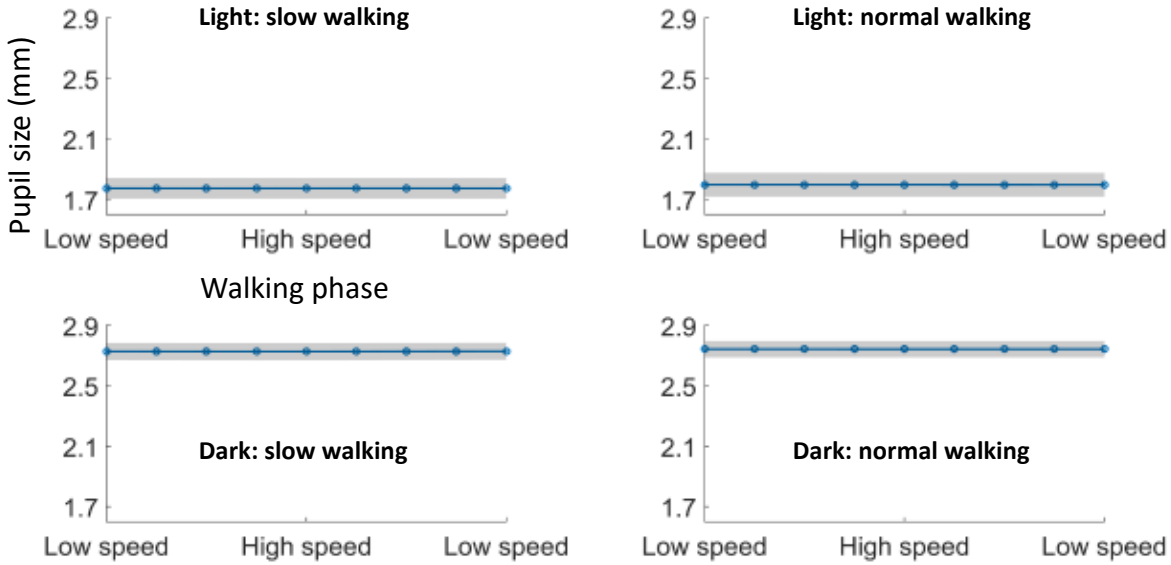


Figure S3. Walking phase does not modulate pupil size. The pupil size did not show any difference in different walking phases. Shading indicates ±1 standard error. N = 27.

3. Study 2: Differential effects of walking across visual cortical processing stages

Differential effects of walking across visual cortical processing stages

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Abstract

Perceptual processes are almost exclusively investigated and understood under marked movement restriction, while natural behaviour includes pronounced movements. Recent human studies have indicated a profound influence of body movement on early visual responses (e.g. evoked components around 100 ms in EEG, electroencephalogram). However, very little is known about the influence of free walking on later visual responses (e.g. responses related to visual selective attention in a later time window than the stimulus evoked N1 component). In the current study, we measured neural signals (EEG) and behavioural performance in a visual selective attention task while participants were standing or freely walking. The results showed that walking was associated with an amplification of

early sensory-evoked potential as indicated by the N1 component. Interestingly, neural indexes of the succeeding processing stages of stimulus discrimination and identification, namely the N2pc component and alpha oscillations, and the eventual behavioural measures were comparable between standing and walking. Additionally, in both standing and walking conditions, an overall advantage in target processing for the right visual field was observed. Our work provides evidence that the early sensory processing is enhanced during locomotion while the succeeding processing steps in a later time window are not modulated by locomotion. We conclude that walking has differential effects across visual cortical processing stages.

Keywords: Alpha lateralisation; Free walking; Mobile EEG; N2pc; Selective attention

3.1 **Introduction**

An important goal in vision research is to understand the visual information processing in natural settings, e.g. during walking (Busse et al., 2017; Parker, Brown, Smear, & Niell, 2020; Saleem, 2020). Human neuroimaging studies have provided us with valuable information about how the human visual system works, but the vast majority of these studies take place under strictly controlled conditions where participants are stationary (i.e. sitting in a chair or lying down in a scanner). Goal-directed behaviour in the natural environment often involves locomotion, and this raises the question of whether these insights into the visual system obtained from stationary participants still hold while participants are in motion (e.g. walking, riding a bike). Recent years have witnessed an increase in the number of studies trying to understand visual information processing during locomotion, a ubiquitous natural situation in which vision is involved. Concerning the early sensory processing, animal studies have provided ample evidence for an amplified magnitude of response to stimuli in the primary visual cortex during locomotion (Ayaz, Saleem, Scholvinck, & Carandini, 2013; Niell & Stryker, 2010; Vinck, Batista-Brito, Knoblich, & Cardin, 2015). Human studies using scalp recorded EEG (electroencephalography) signals, however, provided ambiguous results on this issue. In some studies, early sensory evoked responses around 100 ms following a stimulus onset were found to be enhanced during stationary cycling (Bullock, Cecotti, & Giesbrecht, 2015; Dodwell, Liesefeld, Conci, Müller, & Töllner, 2021) and video gaming (Ki, Parra, & Dmochowski, 2020). However, the enhancement effect of early visual responses was not observed in some other stationary cycling or walking studies (Garrett, Bullock, & Giesbercht, 2021; Malcolm, Foxe, Butler, & De Sanctis, 2015; Nenna, Do, Protzak, & Gramann, 2020; Protzak, Wiczorek, & Gramann, 2021). In a later response time window following a stimulus onset, the P3 component (around 300 ms) was consistently shown to be reduced during locomotion in both visual and auditory domains (Debener, Minow, Emkes, Gandras, & De Vos, 2012; Ladouce, Donaldson, Dudchenko, & Ietswaart, 2019; Nenna et al., 2020; Reiser, Wascher, & Arnau, 2019). For instance, Nenna et al. (2020) showed that walking led to a decrease in the amplitude of P3 compared to standing in a visual discrimination task. In the current study, we will refer to N1 as early sensory responses and responses later than N1 as late sensory responses. Late sensory responses may contain information about transient

cognitive processes that are related to the incoming stimulus, such as the deployment of attention, stimulus discrimination, and target selection.

As a late visual response, the N2pc component is a well-established neural marker of visual selective attention (Heinze, Luck, Mangun, & Hillyard, 1990; Luck, 2012; Luck & Hillyard, 1994a; van Diepen, Miller, Mazaheri, & Geng, 2016). Visual selective attention has an important function in controlling sensory input from the environment to guide human behaviour, thus allowing us to select objects, locations and features for more detailed processing (Kastner & Ungerleider, 2000; Luck & Ford, 1998; Mangun, 1995). In a typical visual task where one target is presented in one hemifield and a distractor in the other hemifield, the N2pc component is defined as a more negative waveform at the contralateral side to the target relative to the ipsilateral side at around 200 ms after the stimulus onset. Besides its well-established role of indexing the attentional selection of targets (Eimer, 1996; Heinze et al., 1990; Jannati, Gaspar, & McDonald, 2013; Mazza, Turatto, Umilta, & Eimer, 2007), the N2pc component has also been discussed as a neural marker of distractor inhibition (Hickey, Di Lollo, & McDonald, 2009; Luck & Hillyard, 1994a, 1994b; Mazza, Turatto, & Caramazza, 2009). In addition to event related potentials, induced oscillatory activity in the alpha band (~10 Hz) has also been proposed as an indicator of attentional distribution (Händel, Haarmeier, & Jensen, 2011; Klimesch, Sauseng, & Hanslmayr, 2007; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; van Diepen et al., 2016), and it is believed to mark inhibitory processes (Jensen & Mazaheri, 2010; Klimesch et al., 2007). Decreased alpha power was shown to predict correct target detection (Van Dijk, Schoffelen, Oostenveld, & Jensen, 2008), while increased alpha power was correlated with the suppression of distracting input (Händel et al., 2011). The lateralisation of alpha activity, i.e. decreased alpha power contralateral to the side of the target, following directed attention cues, is in line with the inhibitory interpretation (Foxe & Snyder, 2011; Händel et al., 2011; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Kelly, Gomez-Ramirez, & Foxe, 2009; Klimesch, 2012; Thut et al., 2006; van Diepen et al., 2016; Volberg, Kliegl, Hanslmayr, & Greenlee, 2009; Worden, Foxe, Wang, & Simpson, 2000; Yamagishi et al., 2003).

To date, the vast majority of studies on visual selective attention were conducted in stationary settings. Given the viability of recording EEG responses during walking (Cao, Chen,

& Händel, 2020; Cao & Händel, 2019; Debener et al., 2012; Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Ladouce et al., 2019), our study aims to understand whether the strength of neural markers shows any difference between standing and walking at different stages of visual processing. This can help to decode the interaction between brain and body movements.

In the current study, we combined mobile EEG recordings and behavioural assessments while participants were tested in a visual selective attention task during both standing and natural walking. In the visual selective attention task, participants searched for a visual target (defined by colour) within a 4-item visual search array and reported the line orientation within the target (Figure ***6***). The results showed an amplified early visual response during walking (indicated by the stimulus evoked N1 component), while the late visual response related to visual selective attention was comparable between movement states (indicated by the N2pc component and the alpha lateralisation). An unaltered visual selective attention process was further strengthened by the behavioural response pattern. Our results indicate that walking has differential effects across visual cortical processing stages.

3.2 Materials and Methods

3.2.1 Participants

31 healthy participants (20 females, 11 males; mean age: 28.4 ± 6.3; 3 left-handed) were recruited from a local participant pool (the SONA system) including both students and no-students. The sample size was determined with two factors taken into consideration: 1. A statistical power of 0.75 should be achieved assuming a medium effect size in a paired t-test; 2. The constraint of available resources. All participants had normal colour vision and normal or corrected-to-normal visual acuity. Informed consent was obtained prior to the study, and each participant received 20 euros as compensation at the end of the study. The protocol was approved by the Research Ethics Committee at the University of Würzburg and was conducted in accordance with the Declaration of Helsinki and the European data protection law (GDPR).

3.2.2 Stimuli and procedure

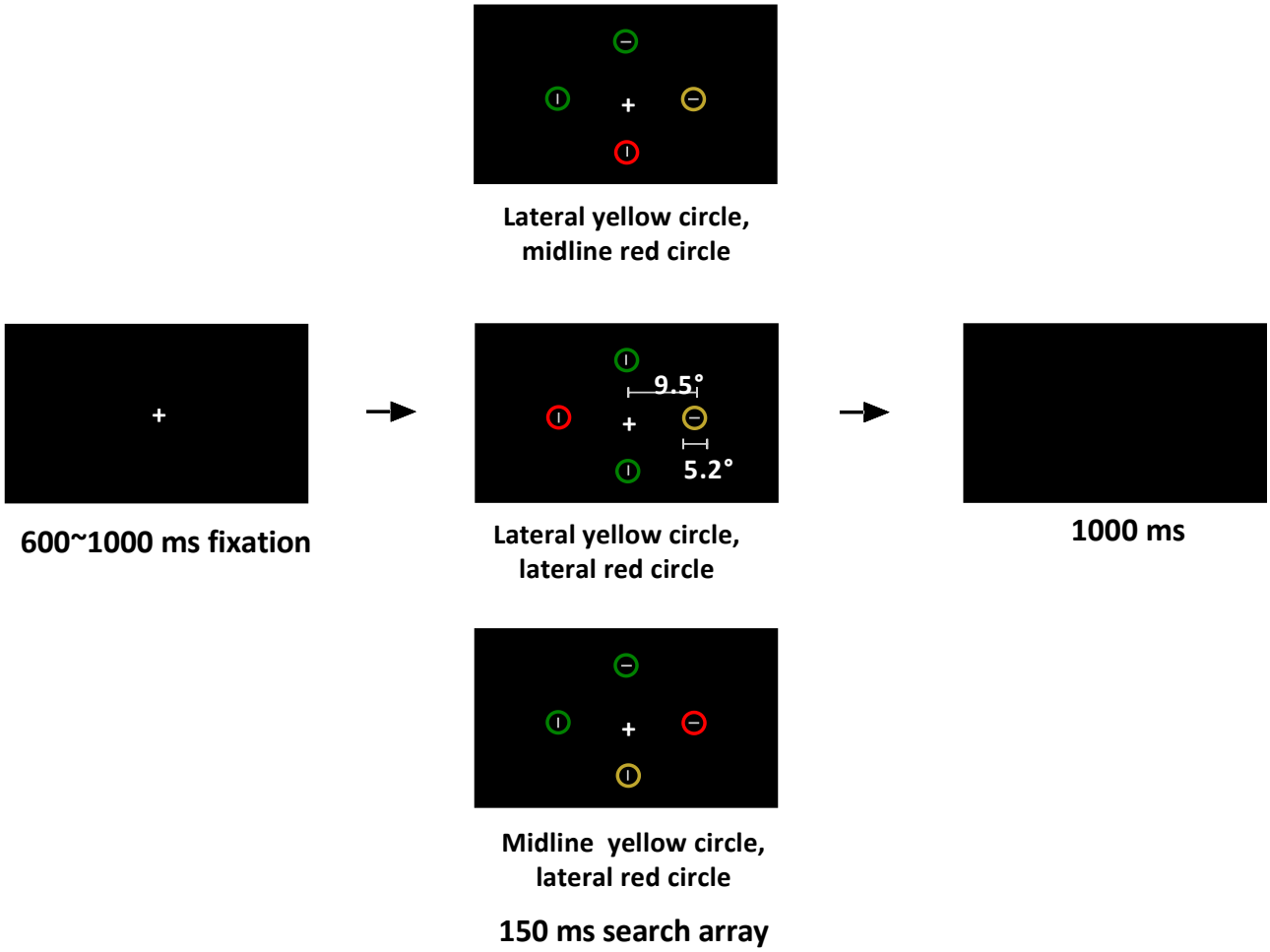

Figure 6. Example sequence of events within a trial. Every trial started with a random fixation interval (600-1000 ms), which was followed by the visual search array (150 ms). In each visual search array, there was always one yellow circle, one red circle, and two green circles. An example of each of the three visual search array categories is given here. The task was to report the line orientation within the yellow circle with a keypress. After the visual search array, another 1000 ms of blank screen was presented before the start of the next trial. Note that the visual stimulus with the target at the midline location was not included in the formal analysis.

Participants completed a line orientation discrimination task in two movement states: standing and walking. The visual stimuli always consisted of 1 yellow circle, 1 red circle, and 2 green circles (Figure ***6***). Each circle had a grey line inside (horizontal or vertical orientation), and participants should report the line orientation inside the yellow target circle using the dominant hand (pressing one button on a handheld response box with the thumb when they

saw a vertical line and pressing another button with the middle finger when they saw a horizontal line). There were 3 types of stimulus configurations based on the relative locations of circles: lateral yellow and midline red; lateral yellow and lateral red; lateral red and midline yellow. In each movement state, 192 trials were included for each stimulus configuration. There were a total of 1152 trials = 2 (movement states) x 3 (stimulus configurations) x 192. Within each stimulus configuration, the same number of trials were included for each possible combination of circle location and line orientation for a balanced stimulus design. For example, in the lateral yellow and midline red category, there were a total of 64 possibilities = 2 (left yellow vs. right yellow) x 2 (up red vs. down red) x 2 (line orientation in the yellow circle) x 2 (line orientation in the red circle) x 2 (line orientation in green circle 1) x 2 (line orientation in green circle 2). Therefore, each possibility included 3 trials.

During the testing, the total 1152 trials were divided into 9 blocks (128 trials each block). In each block, a random selection of 64 trials from the standing condition (without replacement) and 64 trials from the walking condition were tested. In the standing condition, participants were asked to stand still while doing the task. In the walking condition, participants were instructed to walk freely with a normal speed while doing the task. Half of the participants were first tested with the standing condition in each block and the other half with the walking condition first. A self-paced short break was given in between blocks.

The stimuli were presented through a pair of augmented reality glasses with 60 Hz refresh rate (DreamWorld AR, Dream Glass 4K edition; San Mateo, CA). Participants could see the stimuli superimposed on the real-world scene as the AR glasses allowed participants to see through the glasses like seeing through a piece of transparent glass. The experiment was conducted in a dimly light room after the participants had adapted to the dim environment. Only a very vague percept of the surrounding objects in the testing room could be formed, which was enough to guide the walking behaviour.

The sequence of events within a trial is illustrated in Figure ***6***. At the beginning of each trial, a central cross was presented, which participants were required to keep their fixation on throughout the trial. After a random interval between 600 and 1000 ms, the visual stimuli were presented for 150 ms, which were then followed by a blank screen for 1000 ms. Participants were asked to report the grey line orientation inside the yellow circle as quickly

and as accurately as possible via the handheld response box. In the visual stimulus, the 4 unfilled circles were presented equidistant (9.5°) from the central fixation point. Each circle was 5.2° in diameter. The target colour was set to be dark yellow, and the pre-assumed distractor was red. Another two non-target circles were green and originally designed to be neutral stimuli. All stimuli were presented on a uniform black background. Based on the difference in chromaticity space the distance between red and green is larger than between yellow and green (Gaspar & McDonald, 2014). In such design, the red circle is therefore rated as considerably more salient than the green and dark yellow circle (Gaspar, Christie, Prime, Jolicoeur, & McDonald, 2016). No part of the study procedures was pre-registered prior to the research being conducted.

3.2.3 Data recording

EEG data were collected using a Smarting mobile EEG system (mBrainTrain LLC, Serbia), which has 24 recording channels with a sampling rate of 500 Hz. Among the 24 channels, 6 channels (3 channels for each eye: one below and one above the eye, one to the outer canthus) were used for EOG recording, which were included in the independent component analysis (ICA) for removing eye movement artefacts, and 18 channels were used for EEG recording (with 1 electrode on each earlobe for possible re-referencing). A common mode sense active electrode placed between Fz and Cz was used for online reference. The mobile EEG system has the EEG signal amplifier and data transmitter integrated into a little box (82 x 51 x 12 mm; 60 grams), which was attached to the back of the EEG cap. The EEG and EOG data were transmitted via Bluetooth. Stimulus triggers were generated with the software Lab Streaming Layer (https://github.com/sccn/labstreaminglayer), which was also used for collecting and synchronizing the other streams of data (EEG, behavioural data). Stimulus generation and presentation was controlled by MATLAB (The Mathworks Inc, R2019b) with the Psychtoolbox add-on (Kleiner, Brainard, & Pelli, 2007) . A Dell laptop (model: Latitude E7440) was used for the overall implementation of the study. During the experiment, participants carried the laptop in a rucksack.

3.3 Data analysis

3.3.1 Behavioural analysis

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study analyses was pre-registered prior to the research being conducted.

A correct response was registered if participants correctly reported the line orientation within 1600 ms from the onset of the visual stimuli. The accuracy was computed as the percentage of correctly identified trials to total trials. Reaction time data (from stimulus onset to response) were only calculated from correct response trials. Data from 2 participants were excluded from any further analysis because of low accuracy (< 0.6). The accuracy data of the remaining 29 participants were all over 0.75 (M = 0.86; SD = 0.06).

To guide the EEG data analysis, we first performed a two-step analysis with the behavioural data to test whether the red circle indeed worked as a distractor and to compare the distraction effect between the red circle and the green circle. To this end, all the trials were selected in which a green circle was on the opposite side of the yellow circle, i.e. there would always be a red circle and a green circle adjacent to the yellow circle in all these selected trials. This would allow a fair comparison of the distraction effect between the adjacent red and green circles. First, we looked at those trials in which the line orientation was the same between the adjacent red and green circles, which would tell us if the red circle and the green circle together could work as distractors. The mean accuracy and the mean reaction time were separately analysed with a three-way (movement state: standing vs. walking; target location: up, down, left and right; line congruency between the yellow (target) and the distractor circles: congruent vs. incongruent) repeated-measures ANOVA. Throughout the manuscript, a Greenhouse-Geisser correction was performed for ANOVA results where necessary. Critically, incongruent trials had significantly lower accuracy (F(1,28) = 18.27, p < 0.001) and longer reaction time (F(1,28) = 41.15, p < 0.001) than congruent trials, demonstrating that the red and green circles could work together as distractors. Second, we looked at those trials in which the line orientation was different between the adjacent red and green circles, which would tell us if there was a difference in the distraction effect between red and green circles. The same ANOVA analysis was performed with the mean accuracy and the mean reaction time. No significant main effect of line congruency could be

found with either accuracy ($F(1,28) = 2.10$, $p = 0.16$) or reaction time ($F(1,28) = 1.83$, $p = 0.19$), demonstrating that the distraction effects from red and green circles were comparable (see supporting information ***S1*** for details) as the positive effect of congruency of the one distractor counterbalanced the negative effect of the other incongruent distractor.

Results from above were relevant to the following EEG data analysis. In the ERP (Event related potentials) analysis, we planned to follow previous work and analyse the distractor related Pd component (the distractor on one hemifield and a neutral stimulus opposite to it; Gaspar et al., 2016; Gaspelin & Luck, 2018; Hickey et al., 2009), the target related Nt component (the target on one hemifield and a neutral stimulus opposite to it; Hickey et al., 2009), and the N2pc component (the target on one hemifield and the distractor on the opposite hemifield; Hickey et al., 2009; Luck, 2012). However, this analysis approach is based on the assumption that the red circle works as distractor, while the green circle constitutes comparably neutral input. Since the existence of a neutral stimulus cannot be supported from the above analysis, we only focused on the N2pc component while treating both red and green circles as distractors. The analysis was further restricted to trials with a lateral target, as the N2pc component is a brain signal representing lateralised stimuli (for a review, see Luck, 2012). Trials with the target at a midline location were not further considered.

Given the same distraction effects from red and green circles, a three-way (movement state: standing vs. walking; target location: left vs. right; line congruency between the target and the opposite distractor: congruent vs. incongruent) repeated-measures ANOVA was performed with the mean accuracy and the mean reaction time separately. Statistical results are reported as significant when the p value was below 0.05.

3.3.2 EEG - ERP analysis

Among the 29 participants included in the behavioural analysis, the EEG data from 1 participant were incomplete because of data transmission error. The remaining data from the 28 participants were analysed with the Fieldtrip toolbox and in-house scripts using Matlab (The MathWorks Inc., USA). The pre-processing for each participant was implemented in three steps. First, the raw EEG data were first band-pass filtered between 0.1 and 30 Hz using a windowed sinc FIR filter before being epoched into trials ([-600 1000] ms with stimulus

presentation at time 0). All the analyses below were also performed without data filtering, and comparable results were obtained (Supporting information ***S2***). Second, trials were visually checked using the fieldtrip function ft_rejectvisual, and trials with excessive noise were manually excluded based on the variance across all channels. An average of 17.18 trials (*SD* = 6.15) out of the total 1152 trials were rejected in this step (stand with left targets: *M* = 2.82, *SD* = 1.98; stand with right targets: *M* = 3.25, *SD* = 2.70; walk with left targets: *M* = 1.95, *SD* = 1.48; walk with right targets: *M* = 2.36, *SD* = 2.13). Third, ICA was applied to all the remaining trials (mixing all trials in one ICA analysis) to remove eye movements, heartbeat, and muscle related artefacts. Three aspects of information were considered during the artefacts rejection, namely the time-series signal, the signal topography, and the power spectrum of the signal. On average, 5.75 (*SD* = 2.27) artefact components were excluded for each condition.

The EEG data were baseline-corrected by applying a 200 ms pre-stimulus baseline. Each trial was corrected for the polynomial trend using the *detrend* function in Matlab. A difference wave was calculated through subtracting the ipsilateral signal from the contralateral signal for identifying the N2pc component, separately for the left targets (O2-O1) and the right targets (O1-O2). Each difference wave was then compared to the corresponding baseline time window ([-200 0] ms) with a paired sample t-test using cluster correction (Hayasaka, Phan, Liberzon, Worsley, & Nichols, 2004). The amplitude of N2pc was calculated as the average amplitude in the time window of [200 250] ms.

3.3.3 EEG – Time-frequency analysis

Time-frequency analysis was performed on the same EEG epochs used in the ERP analysis to evaluate the temporal evolution of power in different frequencies. Single-trial power was estimated through multiplication in the frequency domain using a sliding window (window length: 500 ms, resulting in a frequency resolution of 2 Hz) shifted in steps of 20 ms starting from -300 ms to 700 ms. A log transformation was used for the baseline correction ([-300 0] ms). An alpha modulation index (MI) was then computed at each time point using the formula as follows:

$$\text{Alpha Modulation Index (alpha MI)} = \frac{\text{(alpha power (right electrode) – alpha power (left electrode))}}{\text{abs (alpha power (right electrode)) + abs (alpha power (left electrode))}}$$

The left and right electrodes used in the alpha MI calculation were O1 and O2, i.e. same as the electrodes used in the ERP analysis. A comparison of alpha MI was performed between the left and right targets at each time point using a paired t-test with a cluster correction to identify potential alpha lateralisation induced by lateral targets. A two-way (movement state: standing vs. walking; target location: left vs. right) repeated-measures ANOVA was then conducted to investigate the effect of movement state and target location in the time window where a significant alpha lateralisation was found. Similar MI analyses were performed with theta band power (4-6 Hz) and beta band power (16-30 Hz) as a control (supporting information ***S3***). To illustrate the pattern of alpha lateralisation in the time window of [460 540] ms across the sensor space, an alpha lateralisation value was calculated for each electrode using the weighted difference between trials with targets on the right and trials with targets on the left (averaging the standing and walking conditions):

$$\text{Alpha lateralisation value (for topography plot)} = \frac{\text{(alpha power (right targets) – alpha power (left targets))}}{\text{abs (alpha power (right targets)) + abs (alpha power (left targets))}}$$

3.3.4 Correlational analyses between ERP components, behavioural performance, and alpha MI

The relationship between the N1 component amplitude and the behavioural performance (accuracy and reaction time) was evaluated through a cross-participant correlation analysis. Similar correlation analyses were also performed with the alpha MI to investigate its functional relevance in cognitive processing.

The relationship between responses in the attention-related ERP component (the N2pc) and responses in alpha MI was also evaluated through a cross-participant correlation analysis, considering some recent reports of a close relationship between the two (Bacigalupo & Luck, 2019; Zhao et al., 2019). Based on the results from the preceding analysis, which showed that the N2pc component was triggered by the right target, the amplitude of the N2pc component and the average alpha MI ([460 540] ms) were evaluated. Data from the standing and walking conditions were collapsed in the correlation analysis as no significant differences between the two states were found. All correlation analyses were performed through the Robust Correlation Toolbox (Pernet, Wilcox, & Rousselet, 2013).

3.4 Results

3.4.1 N1 was enhanced during walking

A clear evoked response to the stimulus onset (i.e. the N1 component ([150 200] ms)) was observed (Figure ***7a, b***), with a similar topography between standing and walking conditions (Figure ***7c***). A two-way (movement state: standing vs. walking; target location: left vs. right) repeated-measures ANOVA with N1 amplitude revealed a significant main effect of movement state ($F(1,27) = 26.44$, $p < 0.001$). The N1 component was larger during walking ($M = -5.63$; $SD = 3.97$) than during standing ($M = -2.91$; $SD = 4.42$). No other effects were significant. The enhanced N1 response during walking could be found in the majority of participants (Figure ***7d***). The correlation analysis showed that the amplitude of N1 component was not correlated with either the accuracy ($r = 0.11$, $p = 0.57$) or the reaction time ($r = 0.08$, $p = 0.68$) in the line discrimination task. Therefore, a clear amplification of early visual responses was found during walking as compared to standing.

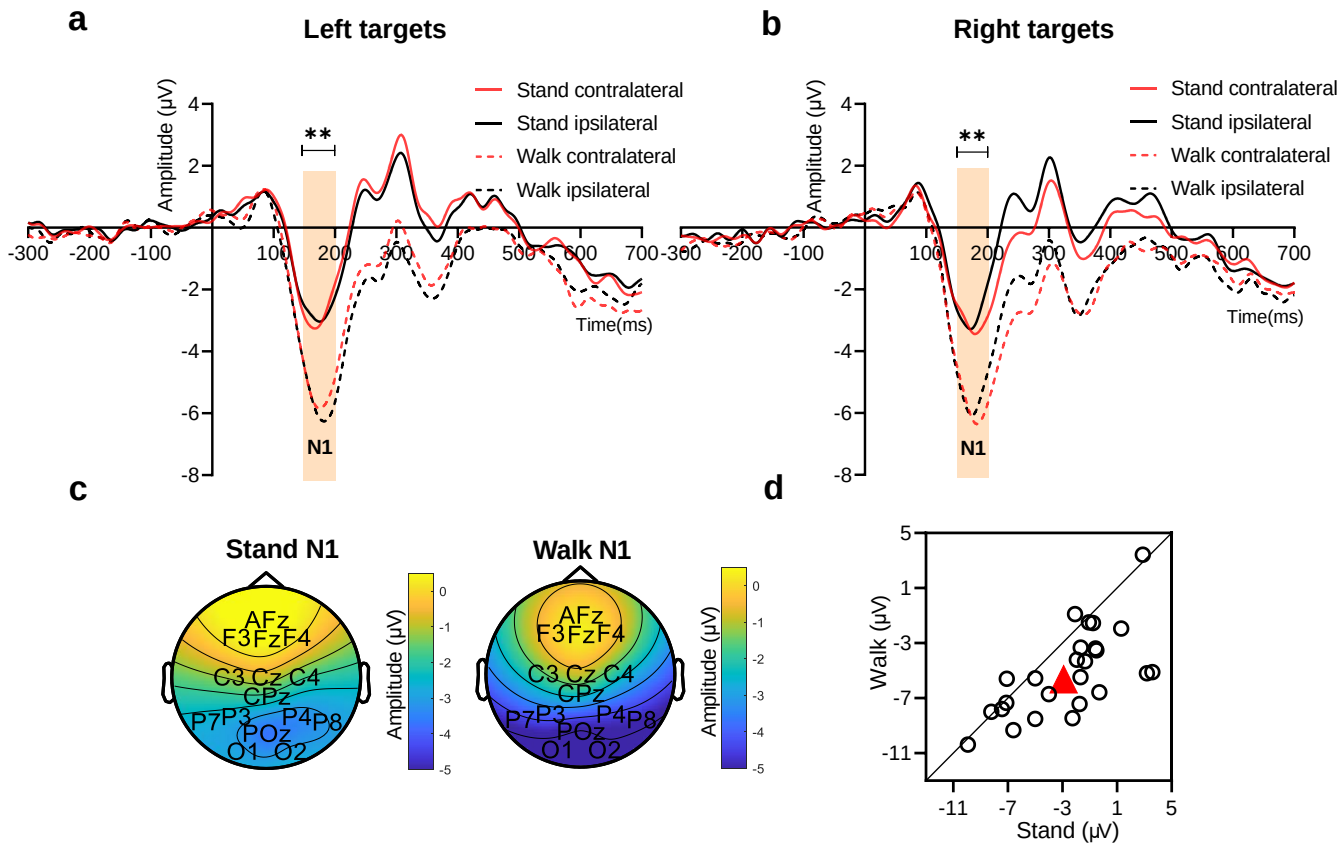

Figure 7. Walking leads to an enhanced visual N1 response. The ERP waveform based on the O1 and O2 electrodes was plotted separately for the left targets (***a***) and the right targets (***b***) at contralateral and ipsilateral sites of the target location in both standing and walking conditions. The shaded box represents the time window of N1 component (yellow). (***c***) The topography of the N1 response ([150 200] ms) was plotted for standing (left panel) and walking (right panel) separately. (***d***) The average amplitude of the N1 component in standing and walking conditions for all participants. 24 (out of 28) participants showed a larger N1 amplitude during walking (under the diagonal). The solid red triangle represents the average amplitude over all participants. *$p < 0.001$

3.4.2 N2pc was comparable between standing and walking

Lateralised targets should lead to a lateralised attentional orientation, which should then be associated with different response patterns between left (O1) and right (O2) electrodes. Therefore, a difference wave was calculated between electrodes O1 and O2 as contralateral-minus-ipsilateral to the target side, separately for the left and right targets in

each movement state, in the aim of detecting attention related responses (Figure ***8a, b***). Each difference wave was then compared to the corresponding baseline time window ([-200 0] ms) with a paired sample t-test using cluster correction. A significant cluster was found in the difference wave for the right target in both standing and walking conditions. The polarity and timing of the cluster fit with the well-known N2pc component (cluster timing: [196 274] ms during standing; [190 302] ms during walking). Therefore, in the following analysis for the lateralized component, the amplitude of the N2pc component was analysed for the right targets and was calculated as the average amplitude in the time window [200 250] ms. The topography of EEG response in the N2pc time window showed a more negative activity for the contralateral electrode (O1) than the ipsilateral electrode (O2) (Figure ***8c***). However, no clear N2pc component could be identified for the left targets in either standing or walking condition.

To evaluate the functional relevance of the N2pc component, we next examined whether N2pc was related to the behavioural performance as marked by reaction time. To this end, trials were categorized into 4 quartiles based on the reaction time to right targets, with Q1 (the first 25%) corresponding to the fastest trials and Q4 (the last 25%) corresponding to the slowest trials. A two-way (movement state: standing vs. walking; reaction time category: Q1 to Q4) repeated-measures ANOVA was then conducted with the amplitude of the N2pc component. A significant main effect of reaction time category was found ($F(3,81) = 3.35$, $p = 0.03$) (Figure ***8d***). Specifically, the amplitude of the N2pc component for fast-response trials (Q1: $M = -1.56$; $SD = 2.42$) was significant larger than for slow-response trials (Q4: $M = -0.63$; $SD = 2.22$) ($p = 0.03$; FDR-corrected post-hoc) (see supporting Figure S7 for the average N2pc difference wave of each reaction time category). No other effects were significant from the ANOVA. Therefore, the identified N2pc component for the right target demonstrated a functional relevance to attentional processing.

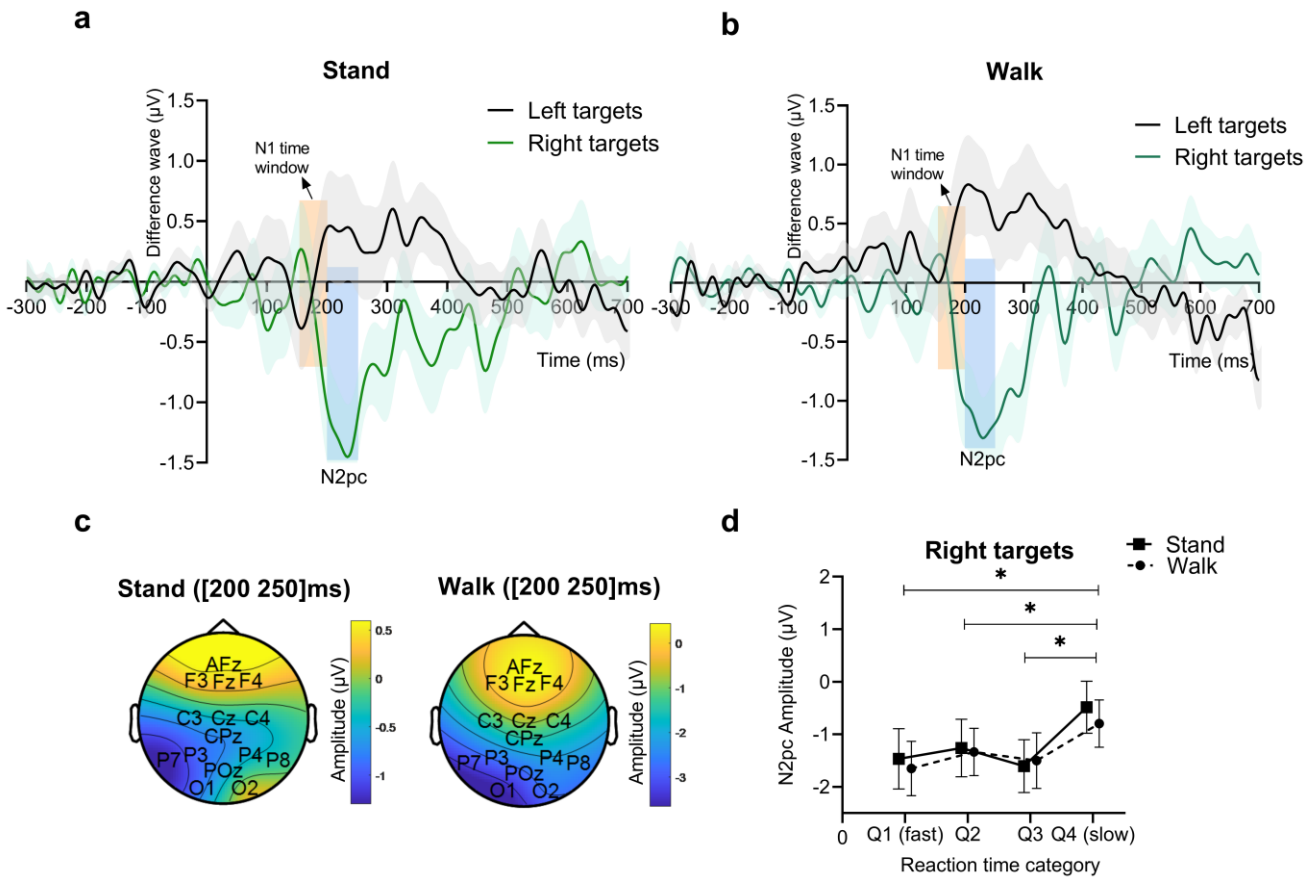

Figure 8. N2pc component was related to reaction time, but unrelated to movement states. For both standing (***a***) and walking (***b***) conditions, a difference wave (subtracting the ipsilateral waveform from the contralateral waveform using O1 and O2 electrodes) was shown for a clear illustration of the N2pc response. Clearly, right targets induced a negative N2pc component (blue box), which cannot be observed for the left targets. The shading indicates ±1 standard error**.** (***c***) The topography of the EEG response in the N2pc time window for standing (left panel) and walking (right panel). The contralateral electrode (O1) had a negative amplitude compared to the ipsilateral electrode (O2). (***d***) For the right targets, trials were sorted into 4 quartiles based on the reaction time to right targets (Q1 to Q4: fast to slow). The fast response trials were associated with a large amplitude of the N2pc component. *$p < 0.05$.

Crucial to the purpose of the current study, we then compared the amplitude of N2pc between movement states. No significant difference was found between standing and walking ($t_{(27)}$ = -0.98, p = 0.34; paired sample t-test). Contrary to the enhancement effect of walking with the early N1 response, it seems that walking does not change the response in a later visual discrimination and identification stage.

3.4.3 Alpha oscillations were comparable between standing and walking and correlated with N2pc

Visual spatial attention is known to be associated with a lateralisation of alpha oscillations, with alpha power being stronger at the ipsilateral side to the target than at the contralateral side (Foxe & Snyder, 2011; Händel et al., 2011; Hanslmayr et al., 2011; Kelly et al., 2009; Klimesch, 2012; Thut et al., 2006; van Diepen et al., 2016; Volberg et al., 2009; Worden et al., 2000; Yamagishi et al., 2003). To explore the role of alpha oscillations in the current work, an alpha modulation index (MI) was calculated as the weighted difference between the right occipital electrode (O2) and the left occipital electrode (O1), separately for left and right targets in each movement state. This should, theoretically, result in a positive MI value for the right targets and a negative MI value for the left targets, i.e. the MI should be larger for the right targets than for the left targets. A point-by-point paired t-test comparison was made with the average alpha MI between the left and right targets (cluster correction). A significant cluster was found in the time window [460 540] ms (Figure ***9a***), showing that the right targets had a larger MI value than the left targets. The topography of alpha lateralisation in this time window also showed a clear reversed pattern between O1 and O2 electrodes (Figure ***9b***). For the right targets, the alpha MI was also significantly correlated with the reaction time (Pearson's r = -0.39, p = 0.04), which indicates a functional relevance of the alpha MI in stimulus processing. Within the time window showing a significant modulation of alpha MI by targets, a two-way (movement state: standing vs. walking; target location: left vs. right) repeated-measures ANOVA was performed to additionally examine the effect of movement state. A significant main effect of target location (F(1,27) = 8.12, p = 0.01) was found, with the right target having a higher alpha MI value (M = 0.11; SD = 0.27) than the left target (M = -0.03; SD = 0.23). No other significant statistical difference was found. Therefore, the alpha lateralisation results corroborate the conclusion from the analysis with lateralised evoked response (the N2pc component) that the late stimulus processing is similar between standing and walking.

We additionally checked whether there was a link between the two temporally separated neural markers, i.e. the N2pc component and the alpha MI. The relationship between the N2pc component and the alpha MI was only examined for the right targets as

the left targets did not have a N2pc component. A negative correlation was found (Pearson's r = - 0.52, p = 0.005; Figure ***9d***), showing that a large N2pc component was associated with a strong alpha lateralisation.

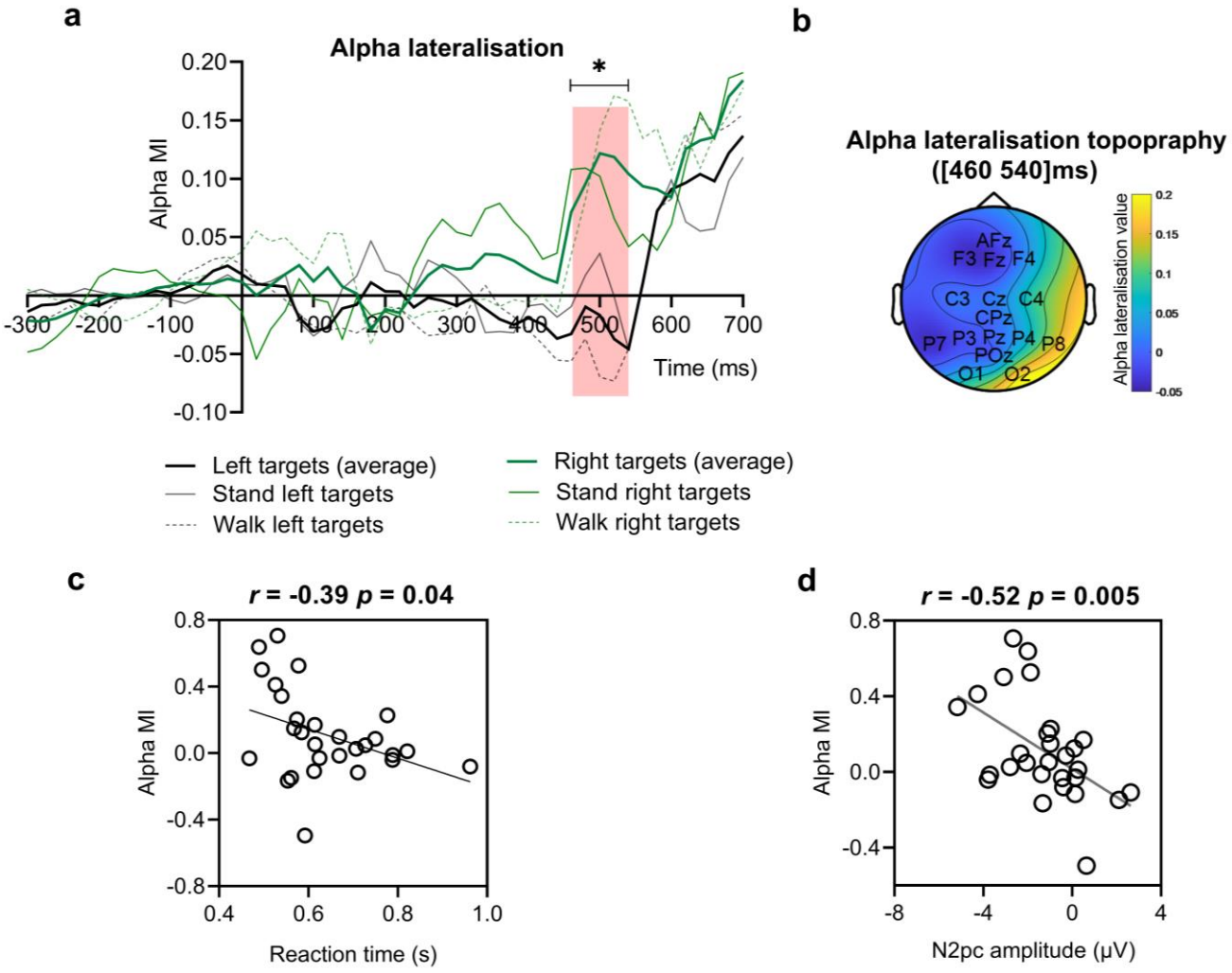

Figure 9. Alpha lateralisation was related to reaction time and N2pc but not modulated by movement states. (***a***) The alpha modulation index (alpha MI; reflecting alpha lateralisation; calculated as the weighted difference between O1 and O2; see Materials and Methods for details) over time is shown separately for the targets from the left visual field (black) and the right visual field (green). Thin lines show the alpha MI separately for standing and walking conditions, and thick lines show the average. The shaded pink area indicates the time window of a significant difference in alpha lateralisation between left and right targets ([460 540] ms). ***(b)*** The topography of the alpha lateralisation in the time window of the shaded pink area in

(a). Note that in the topography plot, the alpha lateralisation value in each sensor was calculated as the weighted difference between left and right targets (see Materials and Methods for details). (***c***) Scatter plot between alpha MI and the reaction time for the right targets. A faster reaction time was associated with a larger alpha lateralisation (indicated by the alpha MI). (***d***) Scatter plot between alpha MI and the N2pc component for the right targets. A larger N2pc amplitude was associated with a larger alpha lateralisation (indicated by the alpha MI). *$p < 0.05$.

3.4.5 The behavioural responses showed a comparable right visual field advantage between standing and walking

As a final step, we checked if the behavioural responses, as a result of stimulus processing, were also comparable between standing and walking. To this end, the response accuracy data were entered into a three-way (movement state: standing vs. walking; target location: left vs. right; line congruency between the target and the opposite distractor: congruent vs. incongruent) repeated-measures ANOVA. A significant main effect of target location was found ($F(1,28) = 5.34$, $p = 0.03$), with a higher accuracy for the right targets ($M = 0.86$; $SD = 0.06$) than for the left targets ($M = 0.84$; $SD = 0.06$), i.e. a right visual field advantage (Figure ***10a***). Crucially, no other effects reached statistical significance, including the main effect of movement state ($F(1,28) = 0.11$, $p = 0.74$). Similar results were obtained with reaction time data. The same ANOVA with reaction time also showed a significant main effect of target location ($F(1,28) = 21.46$, $p < 0.001$), with the right targets leading to a faster response ($M = 0.63$; $SD = 0.12$) than the left targets ($M = 0.66$; $SD = 0.12$) (Figure ***10b***). In addition, a significant main effect of line congruency ($F(1,28) = 7.75$, $p = 0.01$) was found. The main effect of line congruency showed that a congruent line orientation between the target and the distractor ($M = 0.64$; $SD = 0.12$) led to a faster response than an incongruent line orientation ($M = 0.65$; $SD = 0.12$), demonstrating the distraction effect from the opposite distractor. No other effects reached statistical significance, including the main effect of movement state ($F(1,28) = 1.30$, $p = 0.26$).

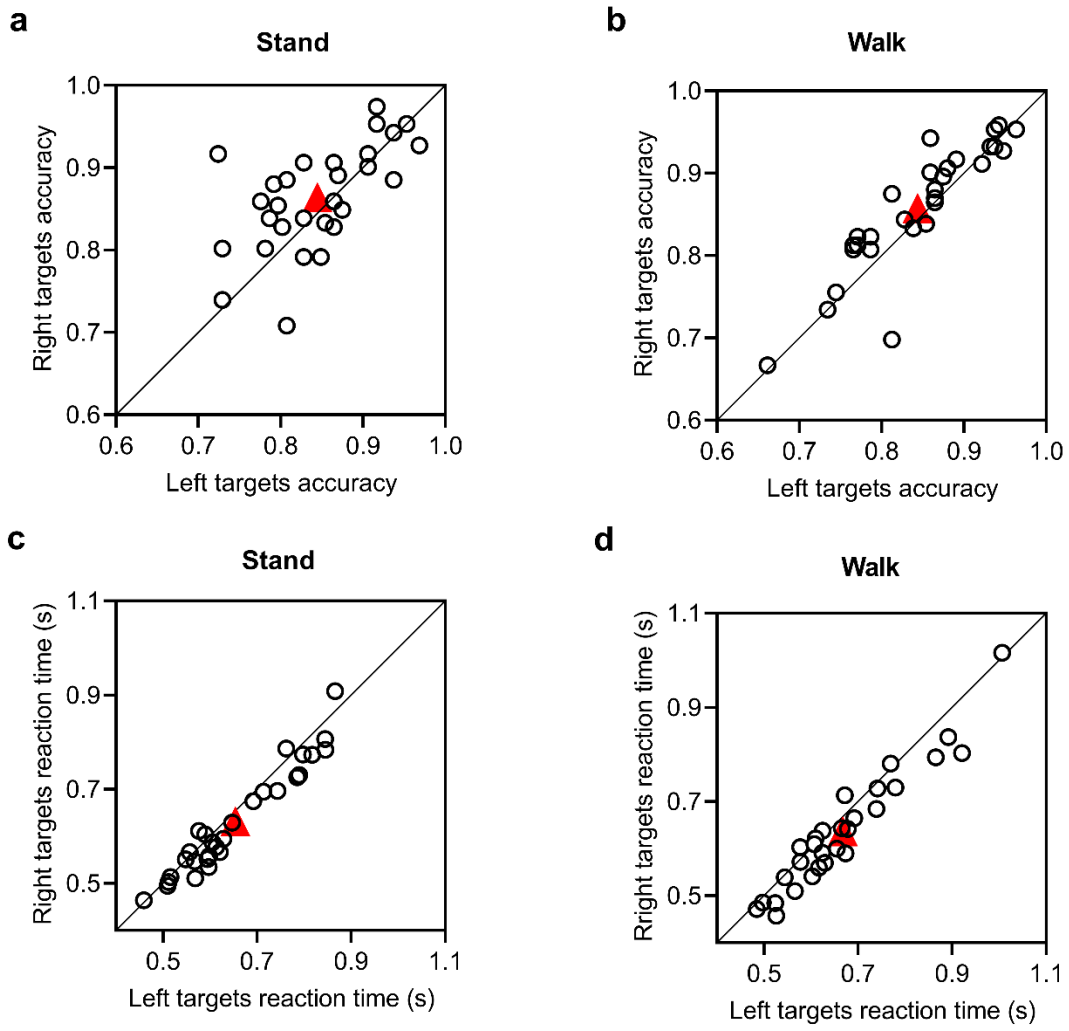

Figure 10. Right targets led to better behavioural performance than left targets. For accuracy, both standing condition (***a***) and walking condition (***b***) showed a better performance for right visual field targets than for left visual field targets. Reaction time data demonstrated the same right visual filed advantage in both standing condition (***c***) and walking condition (***d***), with right targets leading to faster responses. Each circle represents a participant. The solid red triangle represents the average performance. *$p < 0.05$.

3.5 Discussion

In this study, we investigated the process of visual discrimination of an attended target in freely walking participants. The aim was to better understand visual attentional processes during natural behaviour and to bring more ecological validity to previous findings. Our results showed an amplification of the N1 component during walking, reflecting an enhancement of

early sensory processing. This is consistent with findings from animal neurophysiology (Dipoppa et al., 2018; Niell & Stryker, 2010; Saleem, Ayaz, Jeffery, Harris, & Carandini, 2013). In a later processing stage related to visual discrimination and identification, a comparable response was found between standing and walking, with converging evidence from EEG and behavioural measurements. We discuss the implications of the current study in more details below.

Recent animal neurophysiology studies investigating the influence of locomotion on visual processing have consistently shown increased visual responses from the primary visual cortex during locomotion (Dipoppa et al., 2018; Kaneko, Fu, & Stryker, 2017; Niell & Stryker, 2010; Saleem et al., 2013; Vinck et al., 2015). For example, Niell and Stryker (2010) showed that visually evoked firing rates from the primary visual cortex of mice increased by more than 100% from standing still to running. In the current study, a clear enhancement of early sensory processing was found in freely walking humans, which was demonstrated by the increased amplitude of the stimulus evoked N1 component (Figure ***7***). We suggest that the N1 enhancement observed here may have the same neurophysiological underpinnings as the enhanced visual responses observed in animal studies. Indeed, the N1 response was suggested to be related to the excitatory responses of pyramidal neurons (Bruyns-Haylett et al., 2017). Our finding also echoes a recent study showing an increased Ppc component during moderate exercise. The Ppc component is related to pre-attentive processing and has a similar response time window to N1 (Dodwell et al., 2021).

Notably, observing a correspondence between neurophysiological findings in animals through invasive recordings and scalped recorded EEG results in humans is not trivial. There have been previous attempts to replicate the locomotion related response amplification in human EEG studies however resulting in inconsistent findings. For example, while some have demonstrated enhanced early visual processing (indexed by P1 or Ppc component) during moderate intensity stationary cycling compared to a rest condition (Bullock et al., 2015; Dodwell et al., 2021), Garrett et al. (2021) found no evidence of an enhanced early visual processing (P1) during cycling relative to rest when primarily investigating spatial working memory. Albeit Gramann et al. (2010) showed an tendency of early enhancement of the N1 component, the effect was not significant. In addition, studies using the frequency tagging

technique to evaluate visual responses (e.g. a flickering stimulus at 15 Hz leads to increased power at 15 Hz in the EEG signal) also failed to show an enhanced response during walking in general (Benjamin, Wailes-Newson, Ma-Wyatt, Baker, & Wade, 2018; Cao & Händel, 2019; However, see Bullock et al., 2017 for an overall power increase from theta to beta including a 15 Hz SSVEP during stationary cycling). The reasons for the discrepancy can only be speculated at the moment.

One plausible explanation, in our eyes, is related to the difference in the paradigm. The different tasks (e.g. oddball task vs. discrimination task) and stimuli characteristics such as size, luminance, and position, can modulate the global physiological arousal to the sensory information, which could then influence the magnitude of the visually evoked responses (Garrett et al., 2021). A weak visually evoked response might not reliably show external modulations. We indeed noticed that the amplitude of early visual responses in the rest condition (e.g. N1 during standing in the current study, P1 during rest in Bullock et al., 2015) from studies showing an enhancement effect was around or stronger than 3 μV, whereas studies failing to find an enhancement effect typically had a comparably lower amplitude during rest (Garrett et al., 2021; Malcolm et al., 2015; Nenna et al., 2020). A low amplitude could also indicate an overall low signal to noise ratio, suggesting that any locomotion induced change could have been masked by noise. Albeit unlikely, such difference in signal to noise ratio might also be introduced by the use of different EEG recording systems or preparation routines. Another explanation, based on the locomotion type (e.g. overground walking vs. treadmill walking), should not be relevant here because the enhanced visual responses during walking have been reported in studies using different locomotion types (e.g. overground walking in the current study vs. treadmill walking in animal studies). Please note that the divergent findings considering sustained responses (i.e. SSVEP due to frequency tagging) may be due to the stimulus type as a continuously reoccurring sensory input poses different requirements on neural processing compared to a single onset evoking a transient response (i.e. evoked response). This difference might explain why most studies using the frequency tagging technique failed to find an enhancement effect (Benjamin et al., 2018; Cao & Händel, 2019; Dowsett, Dieterich, & Taylor, 2019; Lin, Wang, Wei, & Jung, 2014).

The increased early visual response during walking as compared to standing was not paralleled by a difference in a later processing time window or behavioural performance. Neither the N2pc component nor the alpha lateralisation, both of which are well-established neural markers related to visual attention, showed a difference between standing and walking. The accuracy and reaction time were also similar between movement states. However, both the N2pc component and the alpha lateralisation showed a correlation with the reaction time, indicating their behavioural relevance in this specific task. What is the functional relevance of an increased early visual response during walking but similar attention related responses in visual perception? It has been demonstrated that the high-gain state of the visual cortex during locomotion can facilitate sensory learning (Kaneko et al., 2017) and enhance the information coding of visual stimuli (Dadarlat & Stryker, 2017) in mice. However, especially in a visual selective attention task as employed in the current human study, the interactions might be more complicated. Since the task includes location identification, colour discrimination, spatial attention, distractor suppression, and line orientation discrimination, primary sensory processing might only play a comparably small part in what leads to a successful behavioural response. The enhanced representation of the feedforward information as observed in our experiment, might therefore not lead to an improved behavioural performance.

When looking at the N2pc component in more detail, it is generally thought to be related to attentional target processing (Eimer, 1996; Heinze et al., 1990; Jannati et al., 2013; Kiss, Van Velzen, & Eimer, 2008; Mazza et al., 2007). Indeed, in our data the N2pc component was co-modulated with the reaction time as well as with another neural hallmark of attentional processes, namely the alpha lateralisation. Additionally, we found a correlation between the N2pc component and the alpha modulation index. The lateralisation pattern showed that the alpha power was lower contralateral to the target as compared to the ipsilateral side, a modulation that has been often described to follow attentional orientation and to correlate with behavioural performance (Händel et al., 2011; Sauseng et al., 2005; Thut et al., 2006; Volberg et al., 2009). A co-modulation of the N2pc component and alpha lateralisation strength is expected if both mark an attention-related cognitive process. We therefore suggest that the cognitive processing of stimuli, as indicated by the discrimination

related evoked potentials (the N2pc component), alpha oscillations, and behavioural measures, is comparable between standing and walking.

Interestingly, even specific perceptual features were similarly observed in both standing and walking conditions. Specifically, there is an overall advantage of the right over the left visual field. As described above, we found that the N2pc component was only observable following the target in the right visual field and not the target in left visual field. There is evidence that the left hemisphere is specialised in integrating information concerning the identity of the stimulus (Harter, Aine, & Schroeder, 1982). The target identification process in the current study requires the stimulus identity information as the target is defined by the yellow colour. This could potentially explain why the N2pc component was only observed for the right target (left-hemispheric processing). A similar left-right dissociation of the N2pc component has also been reported in several studies using different stimulus arrangements/materials (Dowdall, Luczak, & Tata, 2012; Eimer, 1996; Wiegand et al., 2018). In the study at hands, the left-right dissociation of the N2pc component was further paralleled by a left-right difference in behavioural performance. Right targets led to a higher accuracy and a faster response than left targets. It should be noted that most participants used their right hand for response, thus giving a possibility that the right visual field advantage may result from the Simon effect (Mazza et al., 2007; Simon & Wolf, 1963). However, a genuine right visual field advantage is support by the following 3 pieces of evidence: 1. The right visual field advantage was observed with the 3 left-handed participants who responded with the left hand (right-minus-left accuracy: 0.12, 0.01, 0.01; right-minus-left reaction time: -0.04, -0.02, -0.01); 2. A right visual field advantage was reported previously using similar tasks with the response hand controlled (Carlei & Kerzel, 2018; Pollmann, 1996, 2000). 3. The current task required pressing one of two response buttons from the responding hand as a response (i.e. a discrimination process is involved). The handedness effect should not have an influence on the accuracy of the response. Therefore, the right visual field advantage seems to reflect a difference on the perceptual level between identifying the left and right targets in this specific paradigm.

3.6 Conclusion

To sum up, we found different effects of movement across visual processing stages. Our study is the first to show a clear enhancement of an early ERP response, reflecting sensory processing, during freely walking, which is consistent with the amplification of neural activities from the primary visual cortex shown in animal studies. Importantly, by using natural walking, this study has increased the ecological validity on the interaction between locomotion and sensory processing. Additionally, we found comparable neuronal and behavioural processes of visual selective attention for standing and walking in a later stage. That both the later cognitive processing and the behavioural output are similar during different movement conditions suggests that the insights on visual selective attention as obtained from constrained lab studies can be generalised to different movement states. Taken together, the complexity of the effect of locomotion should be taken into account when generalising visual processes to natural behaviour, and the difference between early visual processing and the later attention-related cognitive processing needs to be carefully considered.

3.7 Supplementary material (Study 2)

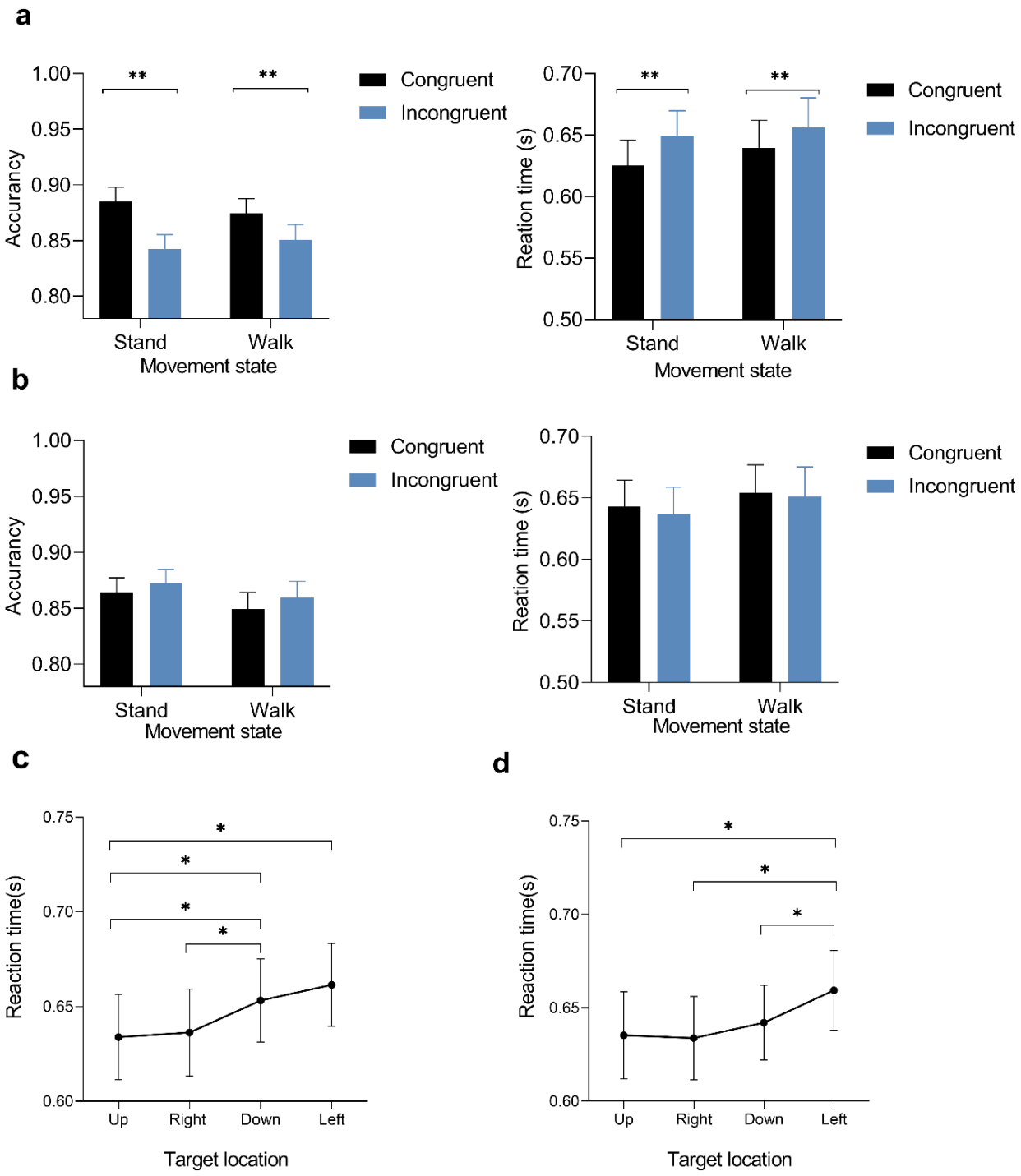

Figure S4. Results of the two-step analysis of the distraction effect from red and green circles. (***a***) Line congruency main effect when the red and green circle had the same line direction as revealed in accuracy and reaction time. (***b***) Line congruency main effect was not significant when the red and green circle had the different line direction. The target location main effect with reaction time when the red and green circle had the different line direction (***c***) The target location main effect with reaction time when the red and green circle had the different line direction. (***d***) The target location main effect with reaction time when the red and green circle had the same direction. * Denotes statistically significant at the $p < .05$ level and** Denotes statistically significant at the $p < .001$ level.

In the first step, we investigated whether the red and green circles together worked as distractors. To this end, trials in which the line direction was the same between the red and green circles were analysed. For accuracy, a three-way (movement state: standing vs. walking; target location: up, down, left and right; line congruency between the yellow and red circles: congruent vs. incongruent) repeated-measures ANOVA showed a significant main effect of line congruency ($F(1,28) = 18.27$, $p < 0.001$) (Figure ***S4a***). The congruent trials had a higher mean accuracy ($M = 0.88$, $SD = 0.06$) than incongruent trials ($M = 0.85$, $SD = 0.06$). No other effects reached statistical significance. For reaction time, the same ANOVA also showed a significant main effect of line congruency ($F(1,28) = 41.15$, $p < 0.001$) with faster reaction times in congruent trials ($M = 0.63$, $SD = 0.11$) than in incongruent trials ($M = 0.65$, $SD = 0.12$) (Figure ***S4b***). Additionally, a significant main effect of target location was found ($F(3,84) = 6.83$, $p < 0.001$) (Figure ***S4c***). The reaction time was fastest when the target appeared in the right visual field ($M = 0.63$, $SD = 0.12$) and slowest when the target appeared in the left visual field ($M = 0.66$, $SD = 0.11$), demonstrating a visual field difference in target discrimination. The above results showed that there was an overall distraction effect from the red and green circles. In the second step, we asked if there was a difference in the distraction effect between the red and green circles. Trials in which the line direction was different between the red and green circles were again analysed with the same three-way ANOVA. For both accuracy and reaction time, the main effect of line congruency was not significant (accuracy: $F(1,28) = 2.10$, $p = 0.158$; reaction time: $F(1,28) = 1.83$, $p = 0.187$), i.e. no evidence showing a differential distraction effect between the red and green distractors. All other significant effects from the ANOVA were reported below for completeness. A significant interaction effect between

movement state, target location and line congruency was found with accuracy ($F(3,84) = 3.47$, $p = 0.020$). A significant main effect of target location was found with reaction time ($F(3,84) = 6.95$, $p < 0.001$) (Figure ***S4d***), again indicating a slow response with the left target ($M = 0.66$, $SD = 0.12$) and a fast response with the right target ($M = 0.63$, $SD = 0.12$).

S5. ERP and time frequency analysis results based on the unfiltered data

A complete ERP and time frequency analysis and corresponding results based on the unfiltered data can also be found below:

The raw unfiltered EEG data were epoched into trials ([-600 1000] ms with stimulus presentation at time 0). The trial rejection for each participant was implemented in two steps. First, trials were visually checked using the fieldtrip function ft_rejectvisual, and trials with excessive noise were manually excluded based on the variance across all channels. An average of 17.18 trials ($SD = 6.15$) out of the total 1152 trials were rejected in this step (stand with left targets: $M = 2.82$, $SD = 1.98$; stand with right targets: $M = 3.25$, $SD = 2.70$; walk with left targets: $M = 1.95$, $SD = 1.48$; walk with right targets: $M = 2.36$, $SD = 2.13$). Second, ICA was applied to all the remaining trials to remove eye movements, heartbeat, and muscle related artefacts. Those artefacts were identified through inspection of the spatial topography, the time-series plot and the power spectrum. An average of 5.82 ($SD = 2.02$) artefact components were excluded for each condition. The EEG data were baseline-corrected by applying a 200 ms pre-stimulus baseline. Each trial was corrected for the polynomial trend using the *detrend* function in Matlab.

N1 component is enhanced during walking

A sensory evoked responses to the stimulus onset (i.e. the N1 ([150 200] ms) component) could be found in occipital electrodes O1 and O2 (Figure ***S5.1a, b***), with a similar topography between standing and walking conditions (Figure ***S5.1c***). A two-way (movement state: standing vs. walking; target location: left vs. right) repeated-measures ANOVA with N1 amplitude revealed a significant main effect of movement state ($F(1,27) = 24.67$, $p < 0.001$). The N1 component was larger during walking ($M = -5.481$; $SD = 4.63$) than during standing ($M = -2.70$; $SD = 5.63$). No other effects were significant. The enhanced amplitudes of the N1

component during walking was also found in the majority of participants (Figure ***S5.1d***), and the amplitude of N1 component not correlated with both the accuracy (r = 0.18, p = 0.36) and reaction time (r = 0.14, p = 0.48). Therefore, a clear amplification of sensory processing-related was found during walking as compared to standing.

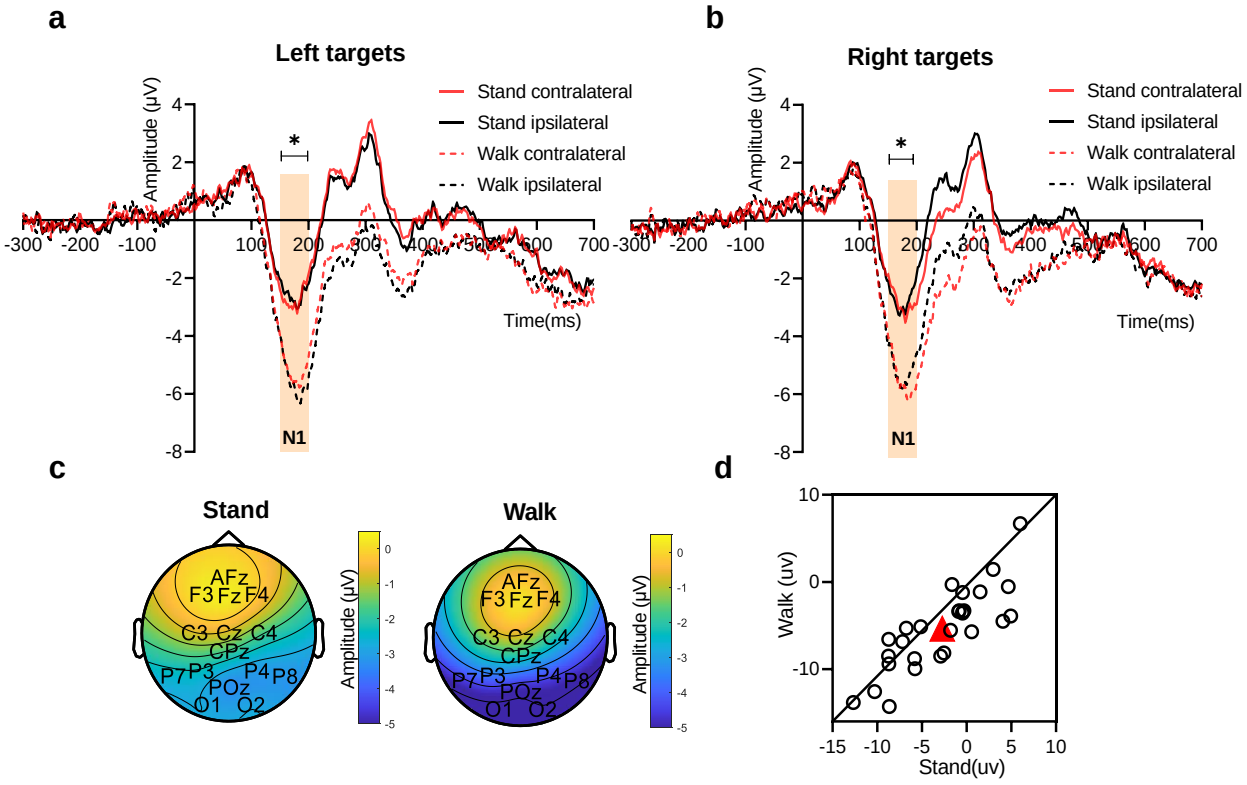

Fig S5.1 Walking leads to enhanced visual N1 component. The ERP waveform was plotted separately for the left targets (***a***) and the right targets (***b***) at contralateral and ipsilateral sites of the target location in both standing and walking conditions. The shaded box represent the time windows of N1 (yellow) components. The topography of the N1 time window were plotted for standing (left panel) and walking (right panel) separately (***c***). (***d***) The average amplitude of the N1 component in standing and walking conditions for all participants, 21 (out of 28) participants showed a larger N1 amplitude during walking (under the diagonal).

The N2pc component is comparable between standing and walking

A difference wave was calculated between electrodes O1 and O2 as contralateral-minus-ipsilateral to the target side, separately for the left and right targets in each movement

state, in the aim of detecting attention related responses (Figure ***S5.2a, b***). Each difference wave was then compared to the corresponding baseline time window ([-200 0] ms) with a paired sample t-test using cluster correction. A significant cluster was found in the difference wave for the right target in both standing and walking conditions. The polarity and timing of the cluster fit with the well-known N2pc component (cluster timing: [212 256] ms during standing; [212 272] ms during walking). However, for the left targets, no clear N2pc component could be observed for either standing or walking. Therefore, in the following analysis for the lateralized component, the amplitude of the N2pc component was analysed for the right targets and was calculated as the average amplitude in the time window [210 260] ms.

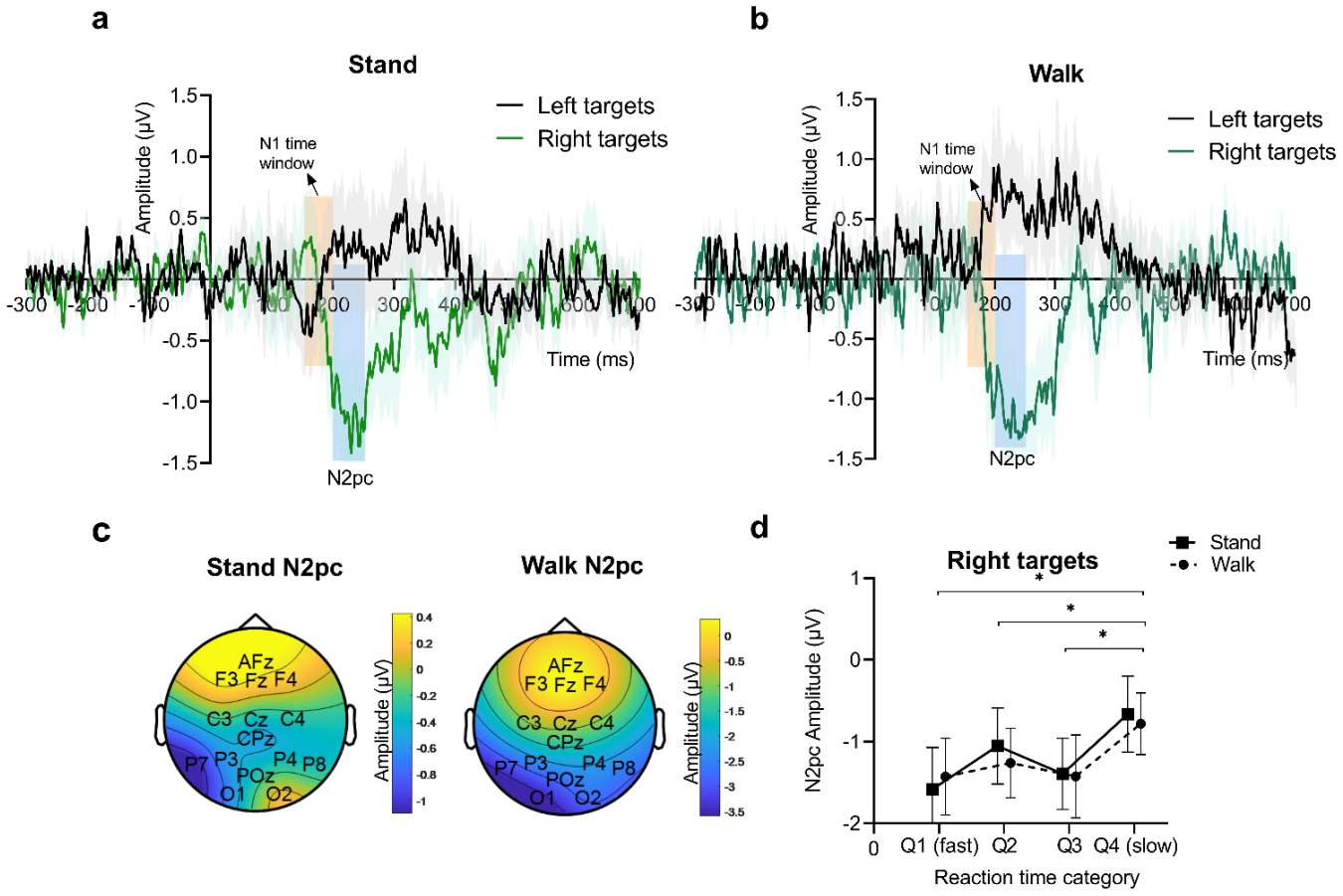

Fig S5.2 The N2pc components are comparable between standing and walking. For both standing (***a***) and walking (***b***) conditions, a difference wave (subtracting the ipsilateral waveform from the contralateral waveform) was shown for a clear illustration of N2pc component for the right targets. The shading indicates ± 1 standard error**.** Clearly, right

targets (green lines) induced a negative N2pc component (blue box), which cannot be observed for the left targets (black lines). (***c)*** The topography of the right targets induced N2pc component time window for standing (left panel) and walking (right panel), the contralateral electrode (O1) had a negative amplitude compared to the ipsilateral electrode (O2). (***d***) For the right targets, trials were sorted into 4 quartiles based on the reaction time responding to targets that appeared in the right visual field (Q1 to Q4: fast to slow), that fast response trials were associated with a large amplitude of the N2pc component. *$p < 0.05$.

To further strengthen the functional relevance of the N2pc component, we next examined whether the identified component was related to the behavioural performance as marked by reaction time. To this end, trials were categorized into 4 quartiles based on the reaction time to right targets, with Q1 (the first 25%) corresponding to the fastest trials and Q4 (the last 25%) corresponding to the slowest trials. A two-way (movement state: standing vs. walking; reaction time category: Q1 to Q4) repeated-measures ANOVA was then conducted with the amplitude of the N2pc component. A significant main effect of reaction time category was found ($F(3,81) = 3.10$, $p = 0.04$) (Figure ***S5.2d***). Specifically, the amplitude of the N2pc component for fast-response trials (Q1: $M = -1.53$; $SD = 2.14$) was significant larger than for slow-response trials (Q4: $M = -0.79$; $SD = 2.11$) (p=0.03, FDR-corrected post-hoc). No other effects were significant from the ANOVA.

We also compared the N2pc component amplitude between movement states. No significant difference was found between standing and walking for the amplitude of the N2pc component ($t_{(27)} = -1.08$, $p = 0.29$; paired sample t-test).

Alpha oscillations were comparable between standing and walking and correlated with N2pc

An alpha modulation index (MI) was calculated as the weighted difference between the right occipital electrode (O2) and the left occipital electrode (O1), separately for left and right targets in each movement state. A point-by-point paired t-test comparison was made with the average alpha MI between the left and right targets (cluster correction). A significant cluster was found in the time window [500 540] ms (Figure ***S5.3a***), showing that the right target had a larger MI value than the left target. From the topography, a clear alpha

lateralisation is visible (Figure ***S5.3b***). For the right targets, the alpha MI was also significant related to the reaction time (Pearson's r = -0.51, p = 0.004, showing a functional relevance of the cognitive processing in a later time window (Figure ***S5.3c***). Within the time window showing a significant modulation of alpha MI by targets, a two-way (movement state: standing vs. walking; target location: left vs. right) repeated-measures ANOVA was performed to additionally examine the effect of movement state. A significant main effect of target location (F(1,27) = 12.24, p = 0.001) was found, with the right target having a higher alpha MI value (M = 0.14; SD = 0.24) than the left target (M = - 0.04; SD = 0.26). No other significant statistical difference was found, suggesting a similar alpha lateralisation pattern between standing and walking. Therefore, the alpha lateralisation results corroborate the conclusion from the analysis with lateralised N2pc component that the attentional orientation process is similar between standing and walking.

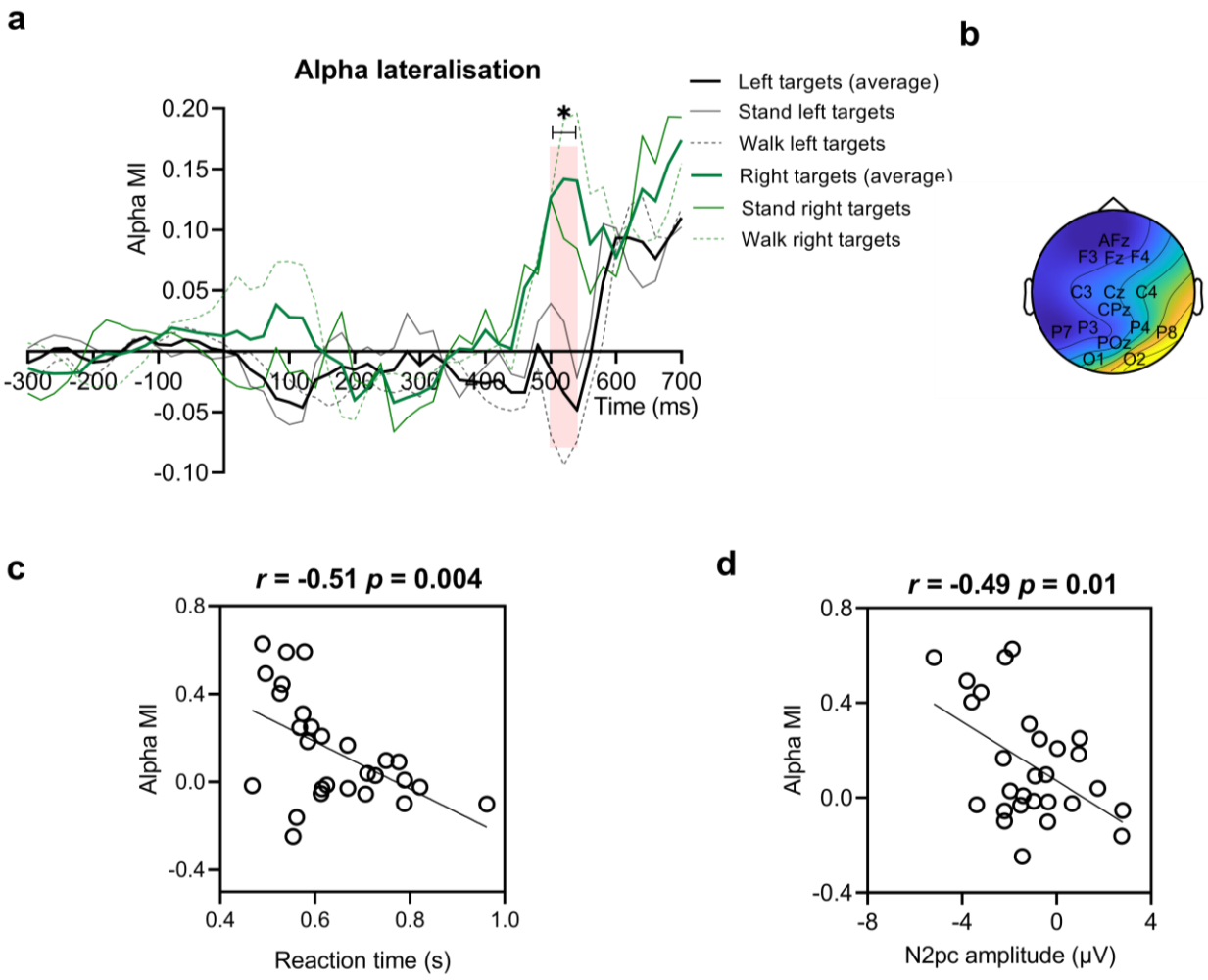

Fig S5.3 Alpha lateralisation results. (***a***) The alpha lateralisation over time (indicated by the modulation index; MI) is shown separately for the targets from the left visual field (black) and the right visual field (green), with the semi-transparent lines showing the same information in both standing and walking conditions. The shaded pink area indicates the time window of a significant difference in alpha lateralisation between left and right targets***. (b)*** The average alpha lateralisation topography during ([500 540] ms) of between standing and walking. (***c***) Scatter plot between the alpha lateralisation and the reaction time for the right target showed is significantly related. A faster reaction time was associated with a larger alpha lateralisation (indicated by the alpha modulation index) (***d***) Scatter plot between the alpha lateralisation and the N2pc component for the right target. A larger N2pc amplitude was associated with a larger alpha lateralisation (indicated by the alpha modulation index). *$p < 0.05$.

The relationship between the N2pc component and the alpha MI was examined for the right targets. A negative correlation was found between the N2pc component and the alpha MI across participants (Pearson's $r = -0.49$, $p = 0.01$; Figure ***S5.3d***), showing that a large N2pc component was associated with a strong alpha lateralisation.

S6.

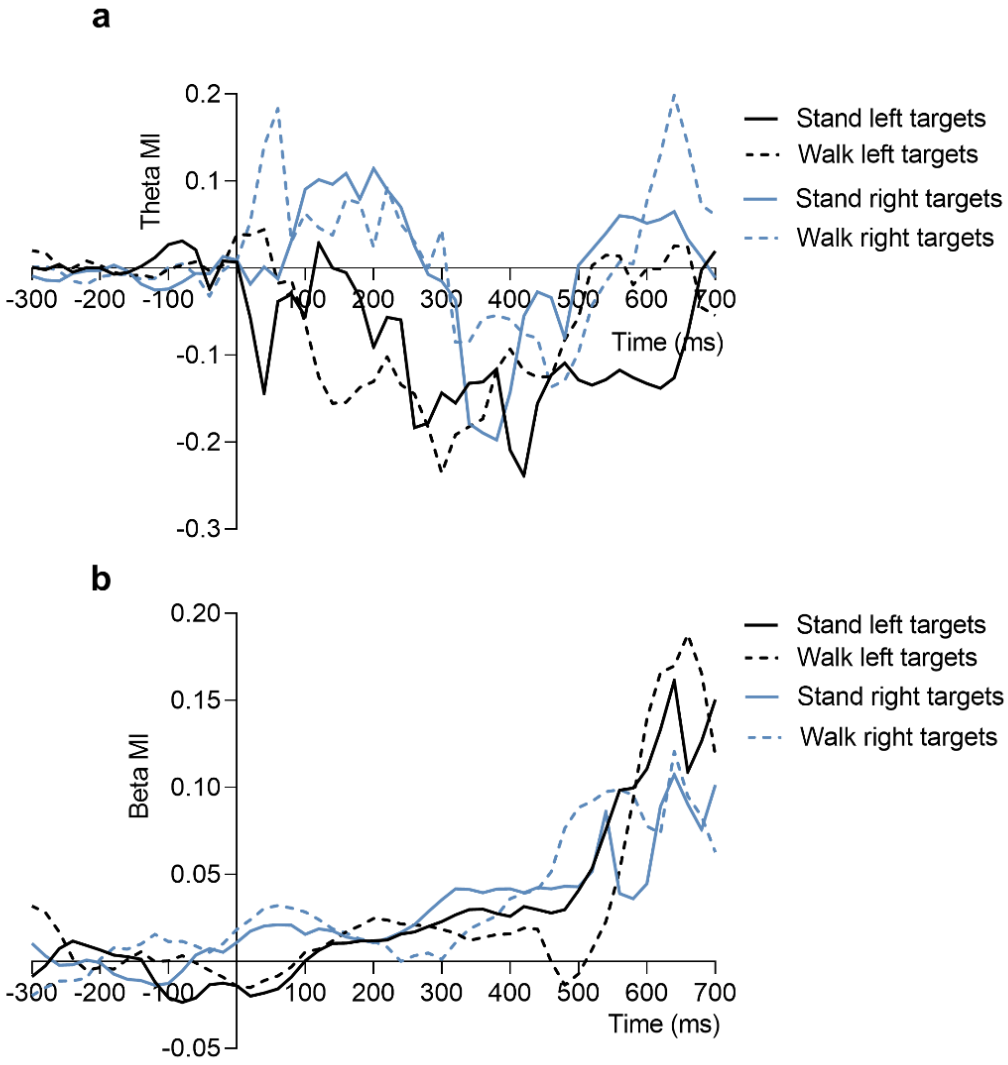

Figure S6. Theta band (4 – 6 Hz) and beta band (16 – 30 Hz) lateralisation at O1 and O2 electrodes. No significant differences in the modulation index were found between left and right targets in either theta or beta band with a cluster correction.

S7.

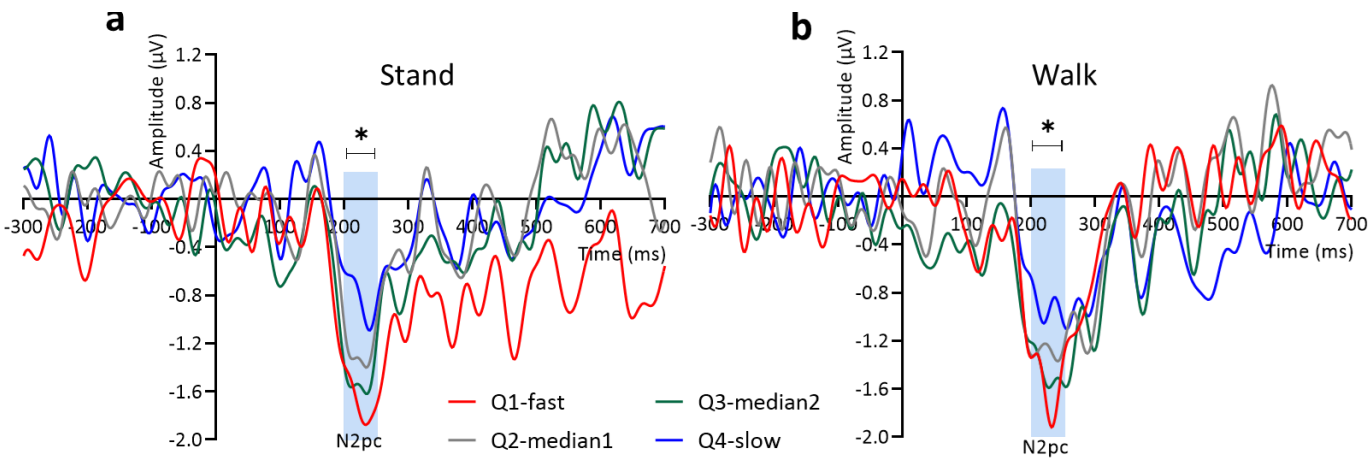

Figure S7. The N2pc difference waves in each reaction time category. (***a***) The N2pc difference waves were plotted for each reaction time category (Q1 to Q4: fast to slow) during standing condition. (***b***) The N2pc difference waves were plotted for each reaction time category (Q1 to Q4: fast to slow) during walking condition. For both movement states, the amplitude of the N2pc component was larger in fast trials (red line) than in slow trials (blue line)(stand: $t(27) = -2.11$, $p = 0.04$; walk: $t(27) = 2.13$, $p = 0.04$).

4. Study 3: Human visual processing during walking: dissociable pre- and post-stimulus influences

Human visual processing during walking: dissociable pre- and post-stimulus influences

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Abstract

Walking influences visual processing but the underlying mechanism remains poorly understood. In this study, we investigated the influence of walking on pre-stimulus and stimulus-induced visual neural activity and behavioural performance in a discrimination task while participants were standing or freely walking. The results showed dissociable pre- and post-stimulus influences by the movement state. Walking was associated with a reduced pre-

stimulus alpha power, which predicted enhanced N1 and decreased P3 components during walking. This pre-stimulus alpha activity was additionally modulated by time on the task, which was paralleled by a similar behavioural modulation. In contrast, the post-stimulus alpha power was reduced in its modulation due to stimulus onset during walking but showed no evidence of modulation by time on the task. Additionally, stimulus parameters (eccentricity, laterality, distractor presence significantly influenced post-stimulus alpha power, whereas the visually evoked components showed no evidence of such an influence. There was further no evidence of a correlation between pre-stimulus and post stimulus alpha power. We conclude that walking has two dissociable influences on visual processing: while the walking induced reduction in alpha power suggests an attentional state change that relates to visual awareness, the post-stimulus influence on alpha power modulation indicates changed spatial visual processing during walking.

Keywords: Alpha power; Attention; Free walking; Mobile EEG; Visual evoked potentials; Orientation discrimination

4.1 Introduction

Animal studies of visual perception during locomotion have shown motor state related changes in both early and late visual cortical activities (Ayaz, Saleem, Scholvinck, & Carandini, 2013; Busse et al., 2017; Erisken et al., 2014; Mineault, Tring, Trachtenberg, & Ringach, 2016; Niell & Stryker, 2010). In recent years, there is also an increase in human electrophysiological research using various movement tasks (e.g. cycling, treadmill walking, and freely walking) investigating the influence of locomotion on different stages of visual processing (Bullock, Cecotti, & Giesbrecht, 2015; Bullock, Elliott, Serences, & Giesbrecht, 2017; Cao & Händel, 2019; Chen, Cao, & Haendel, 2022; Dodwell, Liesefeld, Conci, Müller, & Töllner, 2021; Garrett, Bullock, & Giesbercht, 2021; Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Ladouce, Donaldson, Dudchenko, & Ietswaart, 2016; Wagner, Solis-Escalante, Scherer, Neuper, & Muller-Putz, 2014). The visual processing stages can be roughly divided into an early and a late processing stage, where the early stage is related to the processing of the physical properties of stimuli and the late stage is related to the cognitive extraction of stimulus information (e.g. discrimination and identification).

For early sensory processing, in line with the animal work that observed a movement related increase in firing rates in the visual cortex (Dipoppa et al., 2018; Kaneko, Fu, & Stryker, 2017; Niell & Stryker, 2010; Vinck, Batista-Brito, Knoblich, & Cardin, 2015), a similar increase of early visual evoked potentials (VEPs) during locomotion in humans was reported recently using mobile EEG (electroencephalogram). For instance, both P1 component (peak ~ 130 ms) and Ppc component (peak: ~ 150ms) have been found to be larger during cycling compared to resting state (Bullock et al., 2015; Dodwell, Liesefeld, Conci, Muller, & Tollner, 2021). A robust N1 (peak~180 ms) component enhancement was further observed during free walking (Chen et al., 2022). In a slightly later time window, studies have revealed a reduction in the P3 component due to movement. Bradford, Lukos, Passaro, Ries, and Ferris (2019) found that walking led to a decreased P3 using a visual oddball task. A similar P3 reduction was found by Nenna, Do, Protzak, and Gramann (2020) using a discrimination task as well as a target detection task (Protzak, Wiczorek, and Gramann (2021). Even though divergent visual stimuli were used in the above-listed studies, walking consistently affected the evoked VEPs, i.e. walking led to increased early visual responses and reduced later visual responses at ~300 ms.

However, the source of the movement-related modulation in sensory processing remains unclear. In the current study, we tested the idea that a general change in alpha oscillations due to movement state can account for the changes in VEPs. Based on the above-mentioned movement-related studies, we specifically focused on the N1 component peaking at ~180 ms and the P3 component peaking at ~ 300 ms.

Previous animal studies have shown that the modulation of early visual cortex by walking speed can be independent of visual input as it persists in complete darkness (Dipoppa et al., 2018; Erisken et al., 2014; Keller, Bonhoeffer, & Hubener, 2012). Similarly, a recent walking study in humans found a movement related alpha power decrease in both light and darkness (Cao, Chen, & Händel, 2020). This suggests that the activity changes introduced by walking have a non-visual basis which can be reflected by alpha power changes. Indeed, the alpha power decrease during walking is a robust effect and has been shown by several groups (Ehinger et al., 2014; Lin, Wang, Wei, & Jung, 2014; Peterson & Ferris, 2018; Storzer et al., 2016; Yokoyama et al., 2021). Albeit the fact that the alpha modulation can be independent of the visual input, a recent finding indicated that the walking related alpha power is associated with a change in the spatial distribution of visual input processing during walking (Cao & Händel, 2019). This could indicate that alpha marks a processing state which is modified by walking. In the study at hands we therefore asked if the alpha activity, as modulated by walking, predicts the changed early VEPs following sensory input. Indeed, in previous studies a correlation between pre-stimulus alpha power and the early VEPs has been described (Brandt & Jansen, 1991; De Blasio & Barry, 2013; Roberts, Fedota, Buzzell, Parasuraman, & McDonald, 2014). While the influence of walking on continuous alpha power as well as early VEPs is known, a relationship between these processes has not been established during walking. This however would constitute an important step in understanding how walking influences early sensory processing.

A second important aspect was to test if the walking induced change in processing is based on a general modulation of state or if it is input specific. If general in nature, the walking induced effect should already be found before stimulus onset and be similar for every stimulus manipulation. In other words, there should be no interaction between stimulus features and movement state. In contrast, the change in the response to sensory input might

be specific to certain aspects of sensory processing. In this case, one should find a significant interaction between stimulus features and movement state, given that the relevant features are indeed included. In order to test this, we manipulated the stimulus with respect to target location, distractor presence and eccentricity. These manipulations were chosen because of the involvement of alpha activity in distractor inhibition (Clayton, Yeung, & Cohen Kadosh, 2015; Foxe & Snyder, 2011; Händel, Haarmeier, & Jensen, 2011; Schroeder, Ball, & Busch, 2018; Wostmann, Alavash, & Obleser, 2019) and the differential effect of walking on neural and behavioural measures over the visual field (Cao & Händel, 2019). The main aim of the study was to understand the relationship between the movement state induced changes in ongoing alpha activity and the amplitude modulation of VEPs. However, in order to further establish this alpha activity as a marker of state, we additionally investigated another state change that is experienced during the course of an experiment. To this end, we analysed the change in alpha power as well as the behaviour over the whole period of the experiment.

To investigate the nature of the effect of movement state on early sensory processing, electrophysiological data and behavioural performance were collected while participants performed a line orientation discrimination task (Figure ***10***) during free walking vs. standing using AR glasses and mobile EEG. Pre-stimulus and post-stimulus neural responses were both investigated as a comparison. We replicated previous findings of an enhanced N1 and a reduced P3 component during walking but further showed that these components were predicted by the pre-stimulus alpha power. Additionally, no evidence was found that the effect of walking was dependent on the stimulus-related factors (target location, distractor presence and eccentricity), therefore suggesting that walking can induce a rather general change in the internal state. Alpha power, which we interpret as a marker of the internal state, was also modulated by time on the task and may be related to a learning effect. This was independently found during movement and stationarity. Besides the general movement related change in state, we found a second, stimulus specific influence of walking. Stimulus induced alpha power showed less modulation during walking throughout the task but was particularly influenced by eccentricity and distractor presence, which was neither predicted by pre-stimulus alpha power nor modulated by time on the task. Our findings indicate dissociable pre- and post-stimulus influences of walking on visual processing. One is marked by pre-stimulus alpha power and predicts the amplitude of early sensory responses to any

visual input. The other is marked by stimulus induced alpha power and is specific for visual features.

4.2 Materials and Methods

4.2.1 Participants

30 healthy adults (21 females, 9 males; age: *M* = 25.37, *SD* = 3.88) with normal or corrected-to-normal visual acuity were recruited from a local participant pool via the SONA system. All participants gave informed consent before the experiment, and they were compensated with 10 euros per hour after the experiment. The experimental protocol was approved by the Research Ethics Committee at the University of Würzburg and complied with the Declaration of Helsinki and the European data protection law (GDPR). All measures also complied with the COVID related hygiene safety concept for Psychological Experiments in the Summer Semester 2020 at the Institute for Psychology (Division for Cognitive Psychology) of Wuerzburg University.

4.2.2 Stimuli and procedure

Participants performed a line orientation discrimination task in two movement states (stand vs. walk). The stimulus manipulation included the target location (left vs. right), distractor presence ("with distractor" (red/green) vs. "no distractor") and stimulus eccentricity (1.3°, 9° and 16°). There was an equal number of trials (32) for each possible combination of stimulus manipulation (36) which resulted in a total of 1152 trials. Trials were presented randomly except for the movement state manipulation, which was grouped in four blocks (each block contained one sub-block of standing and another sub-block of walking, with each sub-block including 144 trials). In the "with distractor" manipulation, the visual search array consisted of a yellow circle marking the target and an opposite green or red circle marking the distractor. There was a grey line inside each circle with a horizontal or vertical orientation (balanced between trials). We manipulated the distractor to be either red or green as the two colours can both work as distractors (Chen et al., 2022). In the "no distractor" manipulation, only a target, i.e. a yellow circle with a grey line inside, was included. All circles were 2.2° in diameter with the eccentricity (the distance between the fixation cross and the

centre of the circle) being 1.3°, 9° or 16°. The two circles in the "with distractor" manipulation were always presented in equal eccentricity. Participants were asked to report the line orientation inside the yellow target circle. Half of the participants used their right hand and the other half used their left hand for the response. Responses were collected using a handheld response box, which has two buttons for indicating the line orientation as vertical or horizontal (thumb press and middle finger press; counterbalanced between participants for response mapping). Both accuracy and reaction time were emphasized as the goal to the participants. Two examples of possible event sequences within a trial are illustrated in Figure ***10***. All stimuli were presented via a pair of augmented reality glasses with a 60 Hz refresh rate (DreamWorld AR, Dream Glass 4K edition; San Mateo, CA). Participants could see through the transparent glasses while the task related stimuli were projected onto the real-world scene (as if floating in the air).

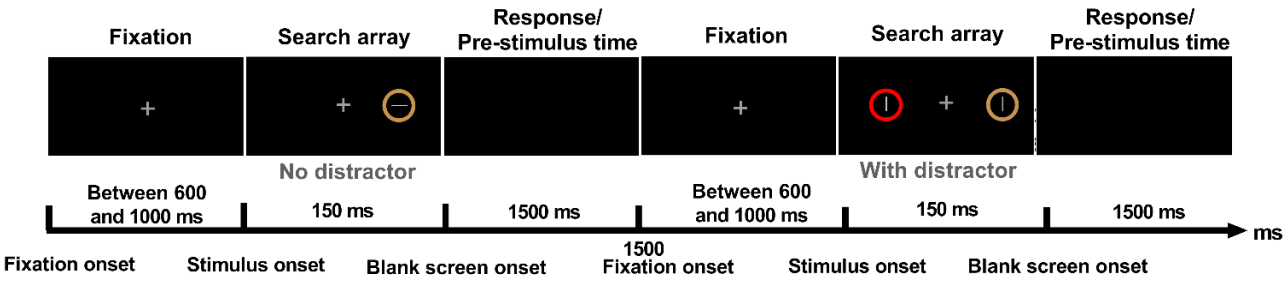

Figure 10. Two possible trial sequences. Every trial started with a fixation interval (duration randomly selected between 600 and 1000 ms) followed by the visual search array (150 ms) that included a yellow circle (the target) with a grey line inside. The target was either displayed alone ("no distractor" manipulation, shown here in the first trial) or accompanied by a distractor which was a grey line inside either a red or a green circle ("with distractor" manipulation, shown here in the second trial). Stimulus manipulations further included the target location (left vs. right) and stimulus eccentricity (1.3°, 9° and 16°). Two examples with an eccentricity of 9° are shown here. After the visual search array, a blank screen was presented for 1500 ms before the start of the next trial, during which participants should report the line orientation within the yellow circle with a keypress as fast and as accurately as possible. Please note that the background is not actually black as participants saw the visual input superimposed on the real-world scene with AR glasses.

The experiment was conducted in a dim and spacious room of approximately 5*6 m. Participants could walk around freely in the room. The dim environment helped to keep the environmental light relatively constant despite the movement. The experiment was conducted in four blocks, each containing a standing a walking sub-block. Over the experiment, all manipulations were balanced between the walking and standing. Trials were randomly placed within the blocks. In the standing manipulation, participants were asked to stand still while doing the task. In the walking manipulation, participants were asked to walk freely at a normal speed while doing the task. Prior to the formal testing, the experimenter showed the participants the normal walking speed (~0.8m/s) and made sure they could follow the required speed by providing feedback in an approximately 1 minute practice session. Half of the participants were first tested with the standing manipulation in each block and the other half with the walking manipulation first. A self-paced short break was given in between blocks. During the whole experiment, the experimenter visually monitored the walking speed making sure there was no significant pace change.

4.2.3 Data recording

EEG data were collected using a Smarting mobile EEG system (mBrainTrain LLC, Serbia), which has 24 recording electrodes with a sampling rate of 500 Hz. Among the 24 electrodes, 6 electrodes (3 electrodes for each eye: one below and one above the eye, one to the outer canthus) were used for electrooculogram (EOG) recording, which were included in the independent component analysis (ICA) for removing eye movement artefacts. Among the remaining 18 electrodes used for EEG recording, 2 electrodes on the two earlobes were used for possible re-referencing, and the other 16 electrodes were distributed according to the standard 10-20 EEG system including the following electrodes: AFz, F3, Fz, F4 (frontal); C3, Cz, C4, CPz (central); P3, P4, P7, P8, Pz, POz (posterior); O1, O2 (occipital). The common mode sense active electrode placed between Fz and Cz was used for online reference. The mobile EEG system has the EEG signal amplifier and data transmitter integrated into a little box (82 x 51 x 12 mm; 60 grams), which was attached to the back of the EEG cap. The EEG and EOG data were transmitted via Bluetooth. Stimulus triggers were generated with the software Lab Streaming Layer (https://github.com/sccn/labstreaminglayer), which was also used for collecting and synchronizing the other streams of data (EEG, behavioural data). Stimulus

generation and presentation was controlled by MATLAB (The Mathworks Inc, R2019b) with the Psychtoolbox add-on (Kleiner, Brainard, & Pelli, 2007). A Dell laptop (model: Latitude E7440) was used for the implementation of the study, which was carried by the participants in a rucksack during the experiment. Therefore, participants were free to move without restriction during the testing.

4.3 Data analysis

4.3.1 Behavioural analysis

Subject exclusion

One participant was excluded due to data transmission error during the experiment. For the remaining 29 participants, a correct response was registered if participants correctly reported the line orientation within 1500 ms from stimulus onset. The accuracy was computed as the ratio of correct response trials to total trials. Reaction time data (from stimulus onset to response) were only calculated for correct response trials. Data from 3 participants were excluded from further analysis because of low accuracy (< 0.6). The remaining 26 participants all had an accuracy over 0.70 (M = 0.87; SD = 0.07).

Main behavioural analysis

The sensitivity measure d' was used, which was calculated as d' = Z(Hit rate) – Z(False alarm rate). We calculated d' separately for targets in the left visual field and targets in the right visual field. Horizontal lines were defined as the signal, and vertical lines were defined as the noise. Hit rate was the ratio of correct response trials to the signal, and false alarm rate was the ratio of incorrect response to the noise. Extreme false alarm rates of 0 were replaced with 0.5/n, and extreme hit rates of 1 were replaced with (n − 0.5)/n (where n is the trial number in each condition) (Macmillan & Kaplan, 1985; Stanislaw & Todorov, 1999).

A four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with vs. no distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA was performed with the d' and the mean reaction time as the dependent variable. Throughout the manuscript, a Greenhouse-Geisser correction was performed for ANOVA

results where necessary. Statistical results are reported as significant when the *p* value was below 0.05.

4.3.2 EEG analysis

ERP analysis

Among the 26 participants included in the behavioural analysis, the EEG data from 1 participant were incomplete because of strong artefacts in the occipital channels (P7, O1 and O2) which could not be fixed. The remaining data from the 25 participants were analysed with the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) and in-house scripts using Matlab (The MathWorks Inc., USA). Because of the low frequency noise, a band-pass filter between [1 30] Hz using a windowed sinc FIR filter was used. In order to exclude potential artificial effects due to the use of a 1 Hz lower bound in signal filtering, all the analyses were also performed with a lower high pass cut-off of 0.1 Hz, which led to qualitatively similar results but were noisier (Supporting information ***S8)***. We therefore reported the results obtained with the 1 Hz lower bound filter. The filtered data were then epoched into trials ([-1000 1500] ms, with stimulus presentation at time 0). Artefact rejection was implemented in two steps. First, trials were visually inspected using the fieldtrip function ft_rejectvisual, and trials with excessive noise were manually excluded based on the variance across channels. Second, the principal component analysis was performed to reduce the spatial dimensionality of the EEG data to 16, which was followed by an ICA to correct for eye movements, heartbeat, and muscle related artefacts. An average of 12.17 trials (*SD* = 8.21; out of the total 1152 trials) and 2.77 artefact components (*SD* = 1.52; out of the total 16 components) were rejected. The EEG data were baseline-corrected by applying a 600 ms pre-stimulus (averaged over -600 to 0 ms) absolute baseline to each trial. The grand average ERP was calculated using 4 electrodes: P7, P8, O1 and O2. The time windows of the N1 and P3 components were selected by using a 50 ms window centring the component peak.

Time-frequency analysis

To evaluate the temporal evolution of alpha power, single-trial power (2 to 30 Hz) was computed based on the multi-taper-convolution method ('mtmconvol' in Fieldtrip) which

uses a sliding window (500ms, in steps of 50 ms starting from -1000 ms to 1500 ms, resulting in a frequency resolution of 2 Hz) with a Hanning taper. The grand average alpha power was averaged over [8 -14] Hz, the range of which covered 22 out of 25 participants' peak alpha frequency (individual peak: *M* = 10.88, *SD* = 1.17). The 3 remaining participants had no visible alpha peak). The same four occipital electrodes as chosen for the ERP analysis (P7, P8 O1 and O2) were used in related alpha power analyses. Alpha power from three time windows was selected for analysis. To test whether the walking related modulation of the stimulus induced alpha changes is influenced by the features of the visual input, we chose a time window of 300 to 450 ms after stimulus onset, as it shows the biggest difference in alpha power between standing and walking via visual inspection. Only for the stimulus induced alpha analysis, we applied a relative baseline correction ([-600 0] ms) using log transformation. This was done to get rid of the movement state related difference in baseline alpha power. The pre-stimulus alpha was selected between 1000 and 1200 ms after the stimulus onset. Note that this pre-stimulus time window was relative to the next trial. The fixation alpha was selected between -200 and 0 ms relative to the stimulus onset.

4.3.3 Within-participants correlational analyses between alpha power, VEPs and behaviour

In order to evaluate the relationship between alpha power, N1, P3, and behavioural performance, within-participants correlation analyses were performed. For each participant (n = 25), the Pearson correlation coefficient (r) was calculated between relevant measures (e.g. alpha power and N1) over the 36 manipulations (i.e. 2 movement states by 2 target locations by 3 distractor scenarios (red/green distractor, no distractor) by 3 stimulus eccentricities; 32 trials in each manipulation). In each manipulation, the relevant measures were calculated as the average over 32 trials. The resulting 25 r values (Fisher's z-transformed) were subject to a one sample t-test against 0 to check statistical significance A significant within-participants correlation was assumed given a t-test result of $p < 0.05$.

We tested three different alpha power types. The stimulus induced alpha power ([300 450] ms, baseline corrected), the pre-stimulus alpha power ([1000 1200] ms) and the alpha power during the fixation period ([-200 0] ms). For the pre-stimulus alpha power, trials with a reaction time > 1000 ms were excluded to exclude the potential influence of motor response on alpha power (excluded trials in each manipulation: *M* = 1.54, *SD* =1.87).

4.3.4 Modulation of alpha power, VEPs and behaviour over time on the task

In order to evaluate the modulation of the alpha power, VEPs and behavioural responses over time, the 32 trials within each of the 36 manipulations were ordered based on the time of presentation and then averaged over all manipulations. In this way, trials from 1 to 32 followed the order of presentation during the testing, however, would not represent an exact time point. Therefore, trial 3 would always be after trial 2 in all manipulations, but trial 3 of manipulation A could be presented before trial 2 of manipulation B. Nevertheless, the correlation between the trial number (time) and the tested variables (pre-stimulus alpha, fixation alpha, stimulus induced alpha, N1 and P3, d', and reaction time) can reveal time dependent changes.

4.4 Results

4.4.1 Behaviour results

Walking led to a decreased d'

To check how movement states interact with target location, distractor presence and eccentricity, the d' data were entered into a four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with distractor vs. no distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA. The main effect of movement state ($F(1,25) = 4.77$, $p = 0.04$) showed a higher d' for the standing condition ($M = 3.10$; $SD = 0.60$) than for the walking condition ($M = 2.92$; $SD = 0.43$). The main effect of distractor presence ($F(1, 25) = 5.99$, $p = 0.02$) showed a higher d' when there was no opposite distractor ($M = 3.10$; $SD = 0.49$) compared with when there was an opposite distractor ($M = 2.92$; $SD = 0.54$), indicating a successful manipulation of the distraction effect. The main effect of eccentricity ($F(2,50) = 8.06$, $p = 0.002$) showed that 16° eccentricity was associated with a lower d' than the other two eccentricities (1.3° : $M = 3.10$; $SD = 0.50$; 9° : $M = 3.10$, $SD = 0.53$; 16°: $M = 2.83$, $SD = 0.55$). We also observed a significant interaction effect between target location and distractor presence ($F(1,25) = 5.82$, $p = 0.02$). In addition, the interaction between movement state, distractor presence, and eccentricity was also significant ($F(2,50)$

= 3.50, p = 0.04), which can be found in Figure ***11a***. Complete test statistics are listed in Table 1.

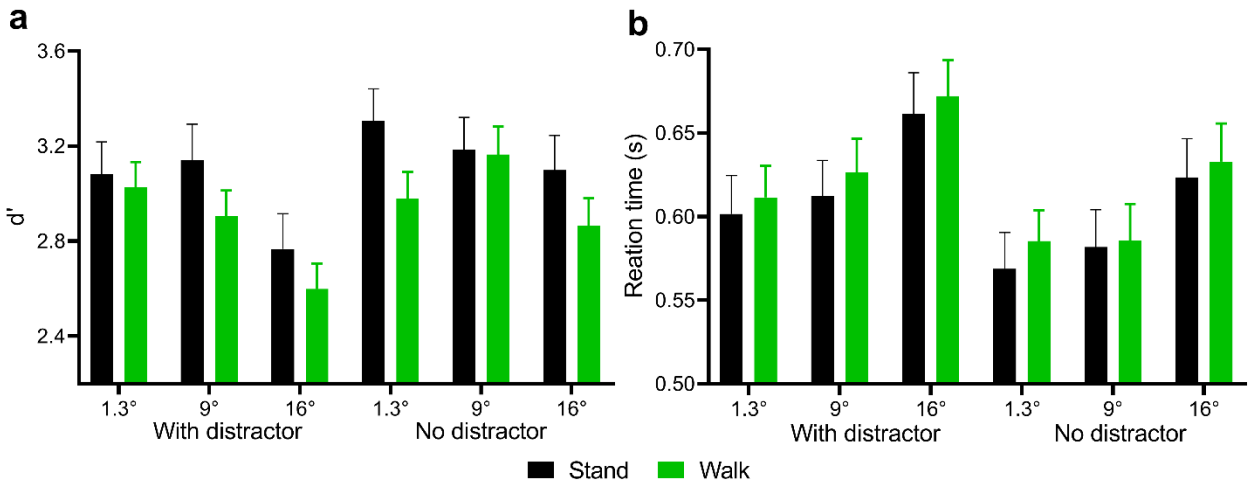

Figure 11. Behavioural performance averaged over target location. Data shown for the d'(a) and the reaction time (b) for each manipulation during standing (black bars) and walking (green bars).

The same analysis using reaction time as dependent variable again revealed a significant main effect of target location ($F(1,25) = 16.04$, $p < 0.001$), with a faster response for the right targets ($M = 0.60$; $SD = 0.11$) than for the left targets ($M = 0.62$; $SD = 0.11$). The main effect of distractor presence was also significant ($F(1,25) = 11.5$, $p < 0.001$), and the reaction time was faster when there was no opposite distractor ($M = 0.60$, $SD = 0.11$) compared to when there was one ($M = 0.63$; $SD = 0.11$), again indicating a successful manipulation of the distraction effect. Also the main effect of eccentricity was significant ($F(2,50) = 85.35$, $p < 0.001$), with the large eccentricity leading to a significantly slower response compared to the smaller two eccentricities (1.3°: $M = 0.59$; $SD = 0.10$; 9°: $M = 0.60$, $SD = 0.11$; 16°: $M = 0.65$, $SD = 0.11$). In contrast to d', there was no significant main effect of movement state on reaction time ($F(1,25) = 1.24$, $p = 0.28$). However, a significant interaction effect between movement state, target location and distractor presence was found ($F(1,25) = 5.33$, $p = 0.03$). No other interaction effects were statistically significant. Complete test statistics are listed in ***Table 1.***

		d’		Reaction time	
Parameter	d.f.	*F*	*p*-value	*F*	*p*-value
Movement state(MS)	1, 25	4.77	**0.04***	1.24	0.28
Target location(TL)	1, 25	2.25	0.15	16.04	**< 0.001****
Distractor presence(DP)	1, 25	5.99	**0.02***	114.98	**< 0.001****
Eccentricity(EC)	2, 50	8.06	**0.003***	85.35	**< 0.001****
MS × TL	1, 25	0.45	0.51	0.02	0.89
MS × DP	1, 25	0.44	0.52	0.07	0.79
MS × EC	2, 50	0.33	0.71	0.31	0.73
TL × DP	1, 25	5.82	**0.02***	0.29	0.60
TL × EC	2, 50	0.76	0.44	1.48	0.24
DP × EC	2, 50	2.08	0.15	1.25	0.29
MS × TL × DP	1, 25	1.04	0.32	5.33	**0.03***
MS × TL × EC	2, 50	1.99	0.15	1.21	0.31
MS × DP × EC	2, 50	3.50	**0.04***	0.97	0.38
TL × DP × EC	2, 50	1.54	0.23	0.46	0.62
MS × TL × DP × EC	2, 50	2.60	0.09	0.03	0.97

Significant effects are indicated in bold. *p<0.05, **p<0.001

Table 1. Results of multifactorial repeated measures ANOVA with d’ and reaction time data.

Taken together, the d’ data showed a reduction in behavioural performance during walking. The interaction between movement state, distractor presence and eccentricity also indicated a changed spatial visual processing during walking. Reaction time largely followed the effects of d’ but showed no main effect of movement state but an interaction between movement state, target location and distractor presence indicating an input specific effect of walking on the behavioural output.

4.4.2 ERP results - Walking led to an early internal-state related processing change

Enhanced N1 response during walking

The amplitude of N1 component was averaged over occipital electrodes (O1, O2, P7 and P8). A four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with distractor vs. no distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA with the N1 amplitude ([170 220] ms) showed a significant main effect of movement state ($F(1,24) = 11.2$, $p = 0.002$) (Figure ***12a-c***). The N1 component was larger during walking ($M = -4.48$, $SD = 3.01$) than during standing ($M = -3.14$; $SD = 2.62$). The main effect of distractor presence was also significant ($F(1, 24) = 4.45$, $p = 0.045$). A stronger N1 was found during "with distractor" manipulation ($M = -4.09$; $SD = 3.19$) than during "no distractor" manipulation ($M = -3.80$; $SD = 3.07$). No other main effects or interaction effects were found statistically significant. To be noted, the N1 enhancement during walking did not interact with any stimulus-related manipulation, including the interaction between movement state and target location ($F(1,24) = 0.03$, $p = 0.95$), the interaction between movement state and distractor presence ($F(1,24) = 0.01$, $p = 0.91$) as well as the interaction between movement state and eccentricity ($F(2,48) = 0.93$, $p = 0.38$). In summary, we find an enhanced N1 response due to walking and due to distractor presence. Importantly, no evidence was found supporting that the effect of movement on was dependent on any external stimulus-related manipulation (target location, distractor presence, and eccentricity).

Reduced P3 response during walking

The posterior P3 component was also tested as to its modulation by movement state, target location, distractor presence, and eccentricity. A four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with distractor vs. no distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA with the P3 amplitude ([270 320] ms) showed only a significant main effect of movement state ($F(1,24) = 7.28$, $p = 0.01$). The P3 component was larger during standing ($M = 1.33$, $SD = 2.60$) than during walking ($M = 0.75$; $SD = 2.57$) (Figure ***12a-c***). No other effects were significant. Similar to the N1 component, no evidence for the dependence of the movement effect on any external stimulus-related manipulation (target location, distractor presence, and eccentricity) was found, as the interaction between movement state and target location ($F(1,24) = 2.40$, $p = 0.10$), the interaction between movement state and distractor presence ($F(1,24) = 1.12$, $p = 0.30$), and

the interaction between movement state and eccentricity ($F(2,48) = 0.99$, $p = 0.37$) all did not reach statistical significance.

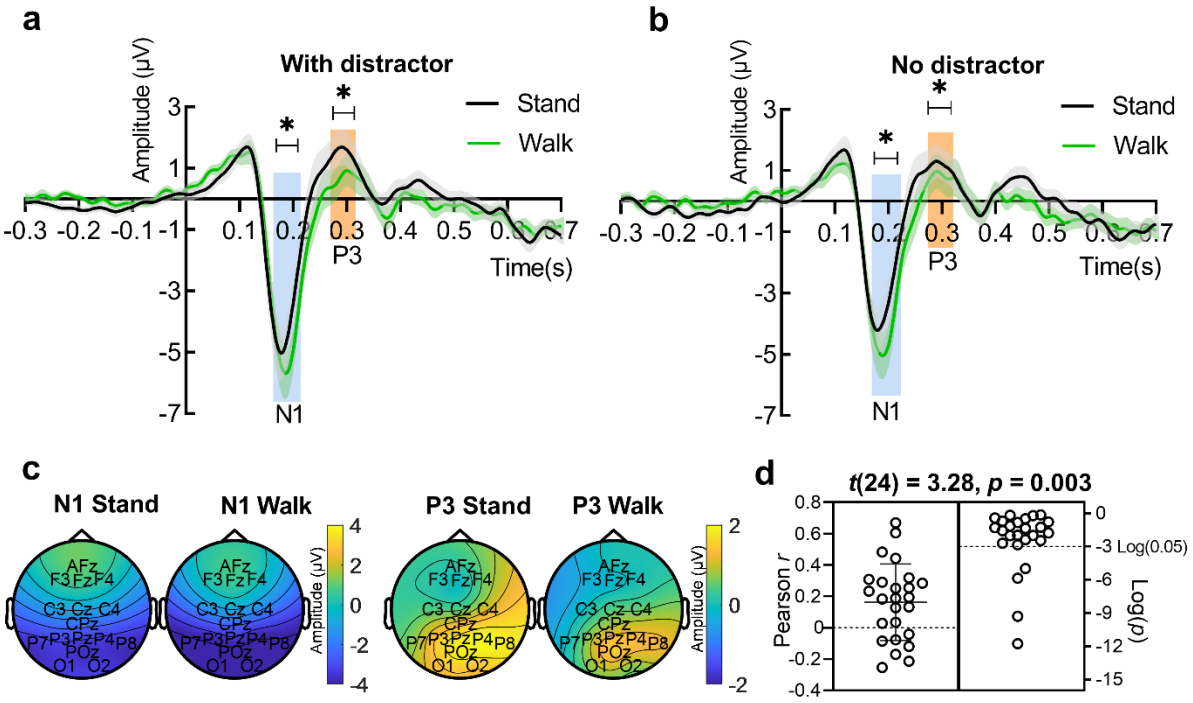

Figure 12. N1 enhancement and P3 decrease during walking. The grand average ERP during standing (black line) and during walking (green line) for (***a***) "with distractor" manipulation and (***b***) "no distractor" manipulation. Data are presented as mean ± SEM (standard error of the mean). (***c***) The topography of the N1 ([170 220] ms) and P3 component ([270 320] ms) for standing and walking separately. (***d***) Within each participant (n = 25), the correlation between the N1 and the P3 component was tested among all 36 manipulations based on the average amplitude of 32 trials in each manipulation. A significant one-sample t-test between the Pearson *r* value (Z-transformed) and 0 (n = 25) indicates a positive correlation between N1 and P3 component. Pearson *r* data correspond to the left y-axis while the *p* value are plotted on a log scale corresponding to the right y-axis. Each circle represents a participant.

The enhanced N1 component and decreased P3 component during walking all did not show any evidence of an interaction with external stimulus manipulation, indicating that the two movement state related effects may have a common origin. To this end, we checked

whether the two components were correlated. The within-participant test based on manipulations showed a significant positive correlation between N1 and P3 component (one-sample t-test between each participant's *r* value and zero: $t(24) = 3.28$, $p = 0.003$) (Figure ***12d***). When testing the behavioural outcome, we found neither a significant within-participants correlation between the N1 amplitude and reaction time ($t(24) = -0.89$, $p = 0.38$) or d' ($t(24) = -0.49$, $p = 0.63$), nor between the P3 amplitude and reaction time ($t(24) = 0.52$, $p = 0.61$) or d'($t(24) = -0.38$, $p = 0.70$).

4.4.3 Pre-stimulus alpha power was reduced during walking and linked to reaction time, N1 and P3 component.

In order to check whether the N1 and P3 changes induced by walking were driven by a general movement-induced state change, we compared the non-baseline corrected pre-stimulus ([1000 1200] ms) and fixation ([-200 0] ms) alpha power (averaged between [8-14] Hz) between standing and walking. Alpha power was taken from the same electrodes (P7, P8, O1 and O2) as chosen for the VEPs and the relationship with VEPs was also analysed. For pre-stimulus alpha power, the results showed a decrease in alpha power during walking ($M = 17.62$, $SD = 12.01$) compared to standing ($M = 24.37$, $SD = 21.39$) ($t(25) = 3.21$, $p = 0.004$) (Figure ***13a***). The topography of the pre-stimulus alpha power showed a difference between standing and walking over posterior-occipital electrodes (Figure ***13b***). We then checked whether the pre-stimulus alpha power was linked to behavioural responses. The within-participants correlation analysis showed a significant correlation between pre-stimulus alpha power and the reaction time (one-sample t-test between each participant's *r* value and zero: $t(24) = -3.27$, $p = 0.003$), with stronger pre-stimulus alpha power linked to a faster response (Figure ***13d***). The correlation between pre-stimulus alpha power and d' was not significant ($t(24) = -1.11$, $p = 0.27$). The same comparison between standing and walking was performed for alpha power during the fixation time window ([-200 0] ms). However, the fixation alpha power neither differed significantly between standing and walking ($t(24) = -0.58$, $p = 0.57$) (Figure ***13c***), nor was correlated with the reaction time ($t(24) = -1.03$, $p = 0.32$).

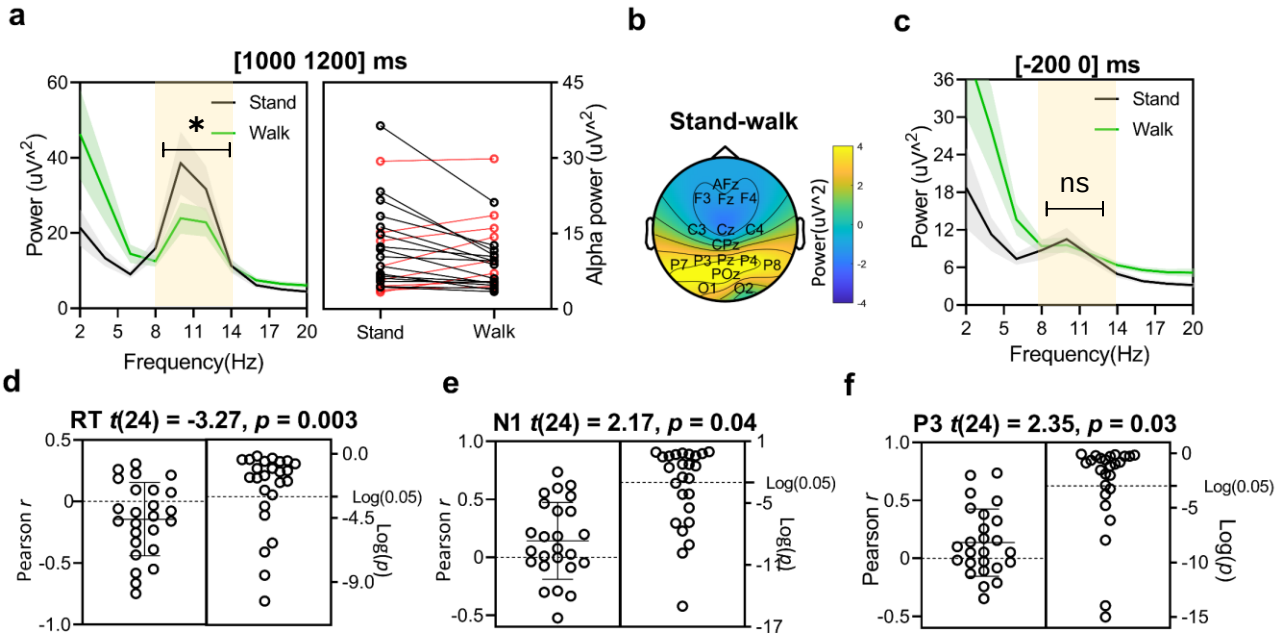

Figure 13. Pre-stimulus alpha power correlated with reaction time and predicted the N1 and P3 components. (***a***) EEG power spectra of the pre-stimulus time window ([1000 1200] ms) for standing (black line) and walking (green line). Data are presented as mean ± SEM (standard error of the mean) (left panel). Alpha power (averaged between [8 -14] Hz) during walking was significantly decreased compared to standing (right panel). (***b***) The topography of the difference between standing and walking (stand-walk) during the pre-stimulus time window. (***c***) EEG power spectra of the fixation time window ([-200 0] ms) for standing (black line) and walking (green line). (***d***) Within each participant (n = 25), the correlation between the pre-stimulus alpha power and the reaction time was tested among all 36 manipulations based on the average amplitude of 32 trials in each manipulation. A significant one-sample t-test between the r value (z-transformed) and 0 (n = 25) indicates a prevalent negative correlation between pre-stimulus alpha power and reaction time. The original Pearson *r* data correspond to the left y axis while the *p* values (log scale) correspond to the right y axis. (***e***) Same as in ***d*** but between pre-stimulus alpha power and the N1 component. (***f***) Same as in ***d*** but between pre-stimulus alpha power and the P3 component.

We further checked whether the movement state-related decrease in pre-stimulus alpha power could predict the N1 and P3 components. The correlations between the pre-stimulus alpha power and the next trial's N1 and P3 components were first examined (based

on all 36 manipulations). As a result, the pre-stimulus alpha power significantly predicted the N1 component (t-test between each participant's *r* value and zero: $t(24) = 2.17$, $p = 0.04$) and the P3 component ($t(24) = 2.35$, $p = 0.03$) (Figure ***13e, f***); The same correlations were also checked for standing and walking separately. Since the within-participants correlation was performed based on the manipulations, the correlation analysis for standing and walking separately led to only 18 sub-manipulations for each participant and each movement state. The correlation between the pre-stimulus alpha power and P3 component was significant for walking ($t(24) = 2.28$, $p = 0.03$) but did not reach statistical significance for standing ($t(24) = 1.61$, $p = 0.12$). The correlation between pre-stimulus alpha and the N1 component for standing ($t(24) = 1.70$, $p = 0.10$) and walking ($t(24) = 1.13$, $p = 0.27$) did not reach significance. However, this probably was due to the reduction in the availability of data when testing separately for each movement state. Same reason might explain the non-significant result when testing for a correlation between pre-stimulus alpha power and reaction time for standing ($t(24) = -0.46$, $p = 0.65$) and walking ($t(24) = -0.75$, $p = 0.46$) separately.

In addition, although we did not find a significant difference between standing and walking in the alpha power during fixation, we nevertheless checked its relationship with the N1 and P3 components. There was no indication that fixation alpha power was correlated with the N1 component ($t(24) = 0.46$, $p = 0.64$) or the P3 component ($t(24) = 0.35$, $p = 0.73$). To summarise, the pre-stimulus alpha power significantly differed between standing and walking and predicted the N1 and P3 components as well as reaction time.

4.4.4 Modulation of alpha power, VEPs and behaviour over time on the task

The overall pre-stimulus alpha power showed a trend to increase with time on the task during both standing and walking (Supporting information ***S2***). To statistically test whether alpha power changeed over time on the task, we investigated how alpha power (fixation and pre-stimulus) and behavioural responses changed from the first trial (1) to the last trial (32). As shown in Figure ***14***, pre-stimulus alpha power increased with time during both standing ($r = 0.88$, $p < 0.001$) and walking ($r = 0.87$, $p < 0.001$) (Figure ***14a***). The increase in alpha power with time corresponded to a behavioural improvement over time: reaction time decreased with time for both standing ($r = 0.57$, $p < 0.001$) and walking ($r = 0.67$, $p < 0.001$) (Figure ***14c***); d' increased with time for both standing ($r = 0.49$, $p = 0.004$) and walking

(r = 0.75, p < 0.001) (Figure ***14d***). However, the fixation alpha power only increased with time during standing (r = 0.79, p < 0.001), but not during walking (r = - 0.01, p = 0.68) (Figure ***14b***).

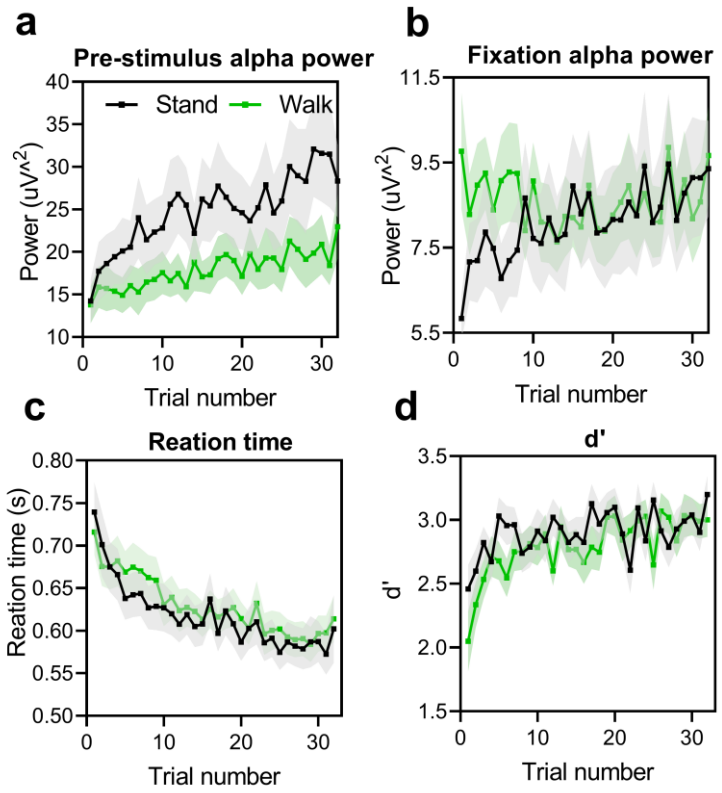

Figure 14. The modulation of alpha power, VEPs and behavioural responses over time on the task. (***a***) Averaged over all manipulations, the pre-stimulus alpha power ([1000 1200] ms) increased with time during both standing (black line) and walking (green line). Each dot represents a trial (1 to 32 trials, ordered by time on the task). (***b***) The fixation alpha power ([-200 0] ms) increased with time during standing but not during walking. (***c***) The reaction time became faster with time similarly for standing and walking. (***d***) The d' also increased with time similarly for standing and walking. Data are presented as mean ± SEM (standard error of the mean).

To check the validity of the time effect, the modulation by time on the N1 and P3 components was also examined. Since pre-stimulus alpha power can predict the N1 and P3 component, we found as expected, that N1 decreased during standing (r = 0.50, p = 0.004) and walking (r = 0.44, p = 0.01) as time increased; P3 increased during standing (r = 0.47, p = 0.01) and walking (r = 0.52, p = 0.002) as time increased.

4.4.5 Stimulus related alpha desynchronisation was smaller during walking and dependent on distractor presence and eccentricity

Alpha power at posterior-occipital electrodes is believed to reflect visual attentional processing with a special role in distractor suppression (Foxe & Snyder, 2011; Händel et al., 2011; van Diepen, Miller, Mazaheri, & Geng, 2016; Van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). Therefore, we investigated the difference of the baseline corrected post-stimulus alpha power (induced by stimulus onset) between standing and walking with respect to spatial attention, distractor suppression and eccentricity of attentional focus. Posterior baseline-corrected alpha power was taken from the same electrodes as used for the ERP analysis (P7, P8, O1 and O2). The time window that demonstrated the clearest alpha power difference between standing and walking was identified through visual inspection of an average over all manipulations ([300 450] ms). The corresponding topography showed an alpha decrease over posterior electrodes (Figure ***15c***). A four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with distractor vs. no distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA was performed with the average alpha power in [300 450] ms. The results revealed a significant main effect of movement state ($F(1, 24) = 4.43$, $p = 0.045$), with standing ($M = -2.48$; $SD = 1.50$) showing a stronger alpha power decrease than walking ($M = -2.07$; $SD = 1.04$) (Figure ***15a,b)***. However, please note that this comparison was circular, as the time window and electrodes were selected based on this difference. All other comparisons from the ANOVA are valid. A significant interaction effect between movement state and distractor presence was observed ($F(1, 24) = 7.02$, $p = 0.01$), showing that alpha power during walking was significantly modulated by the distractor presence while there was no influence of the distractor during standing (Figure ***15d***). When more closely investigating the significant interaction between movement state and eccentricity ($F(2, 48) = 4.13$, $p = 0.03$), we find that particularly at an eccentricity of 1.3°shows a difference of alpha power between two movement states (Figure ***15d***). No other effects were significant.

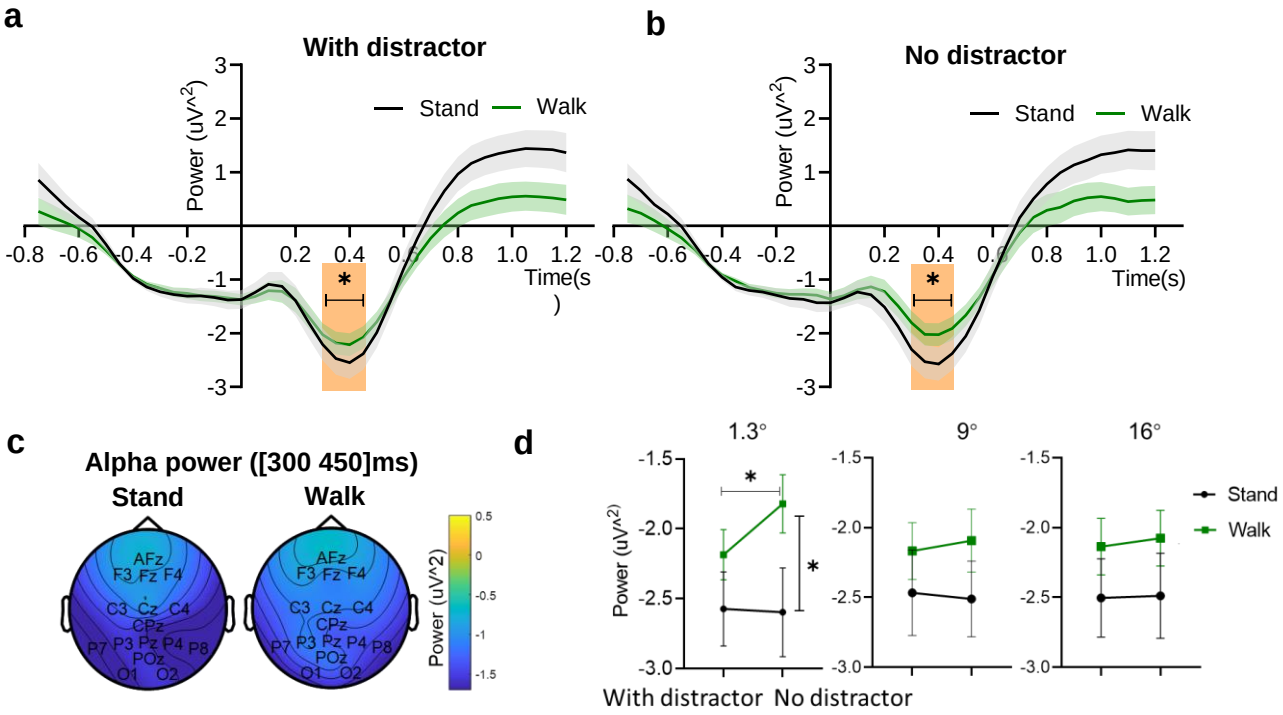

Figure 15. The stimulus related alpha desynchronisation was smaller during walking and affected by distractor presence and eccentricity. (***a***) Baseline corrected alpha power (averaged over [8 -14] Hz, and P7, P8, O1 and O2 electrodes) for standing (black) and walking (green line) for "with distractor" and (***b***) "no distractor" manipulation. The time between [300 450] ms (marked in orange) showed the strongest difference in alpha power between standing and walking. Data are presented as mean ± SEM (standard error of the mean). (***c***) The topography of alpha power ([300 450] ms) during standing (left panel) and walking (right panel). (***d***) The interplay between alpha power and movement state (stand vs. walk), distractor presence (with distractor vs. no distractor) and eccentricity (1.3º vs. 9º vs.16º) is shown. During walking, alpha power was modulated by distractor presence and eccentricity as indicated by significant interactions.

We further investigated whether the stimulus induced alpha power ([300 450] ms) reflected a similar process as the early sensory N1 and P3 amplitude change which was predicted by pre-stimulus alpha power. A within-participant correlation between stimulus induced alpha power and pre-stimulus alpha power was performed. A one-sample t-test between each participant's *r* value and zero did not indicate a prevalent correlation ($t(24) = -1.72$, $p = 0.10$) . Additionally, we did not find an indication for a correlation between stimulus

induced alpha and the N1 ($t(24) = -0.96$, $p = 0.35$), or the P3 component ($t(24) = 0.06$, $p = 0.95$). The stimulus induced alpha power was not modulated by time during both standing ($r = -0.25$, $p = 0.17$) and walking ($r = -0.30$, $p = 0.10$). In summary, we found that the stimulus induced alpha power was less modulated by the stimulus onset during walking compared to standing, and at the same time more strongly influenced by distractor absence and stimulus eccentricity. This stimulus induced alpha power modulation may index a later processing that is distinct from the processing indexed by the pre-stimulus alpha power, N1 and P3 components.

4.5 Discussion

While previous studies have indicated a change in early visual processing during walking, our aim was to investigate whether this change is related to a movement induced general state-change indicated by reduced pre-stimulus alpha activity. We confirmed an enhanced N1 and a reduced P3 component due to walking and replicated the alpha power reduction effect during walking. No evidence was found that the walking related N1 enhancement and P3 reduction were dependent on stimulus-related manipulations (target location, distractor presence and eccentricity). Importantly, we found that the amplitude of the early VEPs could be predicted by pre-stimulus alpha power. In contrast, the stimulus induced alpha power could not be predicted by pre-stimulus alpha power, but showed a stimulus feature specific modulation due to movement. Over the course of the experiment, pre-stimulus alpha power but not stimulus induced alpha power increased, while reaction time decreased and d' increased. Interestingly, the effect of time on task was found similarly for walking and standing suggesting a comparable effect of learning during standing and walking. Overall, the findings suggest that the alpha power change found during pre-stimulus time can mark different internal states but is clearly distinct from stimulus induced alpha indexing specific sensory input processing. The findings will be discussed in detail below.

4.5.1 Enhanced N1 and reduced P3 during walking are linked to an internal-state related processing change

In the current study, we replicated the movement induced change of early VEPs as previously reported in humans (Chen et al., 2022). The increase in the N1 component is likely

related to the increased firing rates in the visual cortex as found in animal studies (Bullock et al., 2015; Dodwell, Liesefeld, Conci, Muller, et al., 2021; Niell & Stryker, 2010; Vinck et al., 2015). Besides the walking related increase, the study at hands found no evidence that the N1 component was affected by stimulus manipulation except for the main effect of distractor presence. The presence of a distractor led to an increased N1 component, which is likely due to the doubling of sensory input as compared to when no distractor was presented. Could an increased sensory input also explain the enhanced N1 component during walking? This is very unlikely as walking adds sensory noise that is not temporally linked to the stimulus onset and therefore should not affect the averaged signal. The P3 decrement during walking was also in line with previous studies showing a decrease in P3 in visual tasks performed during movement (Bradford et al., 2019; De Sanctis, Butler, Malcolm, & Foxe, 2014; Nenna et al., 2020; Richardson, Foxe, Mazurek, Abraham, & Freedman, 2022). In the current study, again, no evidence was found that P3 component was dependent on distractor presence or stimulus eccentricity. This indicates that N1 and P3 share some functionality as they are correlated in amplitude and are both affected by the movement state. Importantly, the lack of interaction between movement state and stimulus features suggests that the change in state due to walking is not specific for certain visual input, but reflects a general change in the way visual input is processed early in the hierarchy of visual processing.

In line with previous studies, we further found a change in ongoing alpha activity during the pre-stimulus time with respect to the movement state. That alpha power is reduced during movement has been reported repeatedly (Ehinger et al., 2014; Lin et al., 2014; Peterson & Ferris, 2018; Storzer et al., 2016). To be more specific, an alpha decrease was found during treadmill walking compared to standing (Lin et al., 2014) as well as during walking compared to stationary cycling (Storzer et al., 2016). Ehinger et al. (2014) reported an alpha suppression specifically during the turning movement in a VR set-up. Previous careful analysis has demonstrated that a change in alpha power during walking can be independent of visual input: Cao and colleagues (Cao et al., 2020) have found that walking in both light and darkness led to a reduced alpha power, which is in line with the animal work (Erisken et al., 2014; Keller et al., 2012). The independence of the modulation of alpha activity from visual input again suggests a general state difference between stationarity and locomotion.

Given the known movement related change in alpha activity (independent of visual input) and the described modulation of VEPs, we investigated whether the pre-stimulus alpha power would predict the strength of visual input processing, indexed by N1 and P3. We found a significant positive correlation between pre-stimulus alpha power and N1 as well as P3, showing that smaller pre-stimulus alpha power led to a stronger N1 and a smaller P3 amplitude. Previous studies have shown that pre-stimulus oscillatory activity can modulate ERP components in various ways and, dependent of the type of oscillation (zero or non-zero mean), can either lead to a reduction in amplitude of all early ERP components or an amplification in late responses (Iemi et al., 2019; Roberts et al., 2014; Zazio, Ruhnau, Weisz, & Wutz, 2022). We find a specific increase only in N1 and P3. Additionally, alpha power affecting the VEP not directly preceded the stimulus onset since pre-stimulus alpha but not alpha during fixation correlated with the VEP component. We therefore conclude, that the walking induced change in alpha power influenced specific visual processing steps. The active inhibition of alpha power might be one mechanism through which walking affects such early visual responses. Whether walking has other ways to modulate visual responses is a question awaiting further studies.

Can we further interpret this movement related state change? Since alpha power has been shown to mark inhibitory processes modulated by attention (Bacigalupo & Luck, 2019; Foxe & Snyder, 2011; Händel et al., 2011; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Sauseng et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Yamagishi et al., 2003), the walking induced modulation of alpha could suggest an attentional process. Additionally, a change in N1 and P3 has been shown to be induced by attentional manipulations (Fedota, McDonald, Roberts, & Parasuraman, 2012; Hong, Wang, Sun, Li, & Tong, 2017; Kapanci, Merks, Rammsayer, & Troche, 2019; Liebherr et al., 2021; Polich & Bondurant, 1997; Slagter, Prinssen, Reteig, & Mazaheri, 2016; Vogel & Luck, 2000; Wascher, Hoffmann, Sanger, & Grosjean, 2009). Following the interpretation of the previously reported link between pre-stimulus alpha and visually evoked components in stationary setups (De Blasio & Barry, 2013), the modulation due to walking might be related to an attentional state change. Note that the attentional state does not refer to ‘directed’ or ‘selective’ attention affecting specific spatial or other features of the input.

Notably, we also found a link between the pre-stimulus alpha power and the reaction time but such correlation was not observed with the d'. In a recent finding, using a letter detection task and additionally including awareness ratings of the target, higher pre-stimulus power predicted lower visual awareness ratings but not discrimination accuracy (Christopher S. Y. Benwell, Coldea, Harvey, & Thut, 2021). The work replicated their previous finding of a link between pre-stimulus alpha power and perceptual awareness but not objective performance (accuracy) in a landmark task (Christopher S Y Benwell, Keitel, Harvey, Gross, & Thut, 2018). The specific link between alpha power and awareness might well explain the correlation between perceptual outcome and pre-stimulus alpha power in certain visual illusions (Händel & Jensen, 2014) or detection tasks (Van Dijk et al., 2008). However, awareness may not necessarily lead to an improvement of every aspect of performance. In our study, the lower alpha power during walking may be associated with a higher awareness, but the task probed the orientation discrimination performance. This might explain why the d' was not correlated with pre-stimulus alpha power or N1 amplitude and why walking showed no improvement in the task related discrimination despite the significant increase in N1 amplitude. Pre-stimulus alpha and the correlated N1 amplitude might however show a correlation with RT based on their link to awareness of the stimulus. Indeed, studies using location detection or change detection tasks found that subjective awareness was associated with an early negative posterior component around 180-280 ms (VAN, visual awareness negativity) which has similar feature as the N1 component in the current study (Koivisto & Grassini, 2016; Koivisto & Revonsuo, 2003).

In summary, we would like to suggest that walking introduces a reduction in alpha activity, marking a disinhibition of cortical activities thereby leading to a stronger N1 component as response to visual input. This modulation (alpha and N1) does not affect spatial or feature based attention but rather increases perceptual awareness. The movement related change in state and the respective change in alpha activity and N1 are therefore not necessarily related to the behavioural outcome of a discrimination task but might well predict awareness. An indicator is the correlation of pre-stimulus alpha power with RT and the absence of a slowing of RT during walking, that might have been expected to parallel the reduction in d' in the walking condition.

4.5.2 Pre-stimulus alpha power is modulated over time

Investigating the effect of time on task, we found another state change marked by pre-stimulus alpha power. Over the course of the experiment, pre-stimulus alpha power increased, while reaction time decreased and d' increased. Similar changes over time have been described before: Toosi, Tousi, and Esteky (2017) showed a significant increase in pre-stimulus alpha power from early to the late trials in the predictable discrimination blocks. The increase was also accompanied by an increase in accuracy (see their Figure ***12***) and was interpreted as a consequence of perceptual learning. A similar increase in power with training was also found in somatosensory alpha (Brickwedde, Kruger, & Dinse, 2019), and the alpha power was interpreted as neural marker of perceptual learning efficiency. Indeed, the link between alpha power and learning has been indicated even earlier and was also suggested to be independent of stimulus features (e.g. predictable or not, trained or not). Bays, Visscher, Le Dantec, and Seitz (2015) found an increase in pre-stimulus alpha power in both trained stimuli and untrained stimuli, suggesting automaticity in perceptual learning. Our finding of the time modulation on pre-stimulus alpha power with unpredictable and non-cued stimuli is also in line with the stimuli independent learning hypothesis (Bays et al., 2015).

Importantly, the effect of time on task was found during both standing and walking, indicating that independent of the interpretation of this timing effect, the improvement in a task over time is present throughout different movement states. This suggests that movement has no detrimental effect on learning. However, interestingly, there was one difference in the effect of time on alpha power between the movement conditions. While during walking, the correlation was only visible for the pre-stimulus period, during the standing manipulation, such correlation was also significant for the fixation period. This could mean that during walking we do not change our response to the initial stimulus appearance. While during non-movement manipulation, we adapt all responses to the task. In other words, while during stationarity, we allow the neural response to visual onset (as the post-stimulus alpha likely marks attention towards the input) to adapt with time, but the response to visual input during walking will not be modulated but kept constant no matter what visual task is additionally executed. Ecologically, this interpretation makes sense as it is likely always

advisable to react to visual input when walking so as not to run into objects or to modify the path according to the new information.

4.5.3 Stimulus induced alpha power is less modulated during walking and accompanied with a significant modulation by distractor presence and eccentricity

Besides the pre-stimulus alpha activity, we also investigated the alpha activity induced by the target onset. We found an overall reduced modulation of induced alpha activity during walking. One reason might be that the overall alpha power is lower during walking than standing, which might in turn lead to less modulation by sensory input. However, surprisingly, the exogenous factors related to the stimulus (distractor presence and eccentricity) had a significant effect on alpha power modulation during walking while they had little effect on alpha modulation during standing. Particularly, the eccentricity of 1.3° and no distractor manipulation showed a strongly reduced modulation of alpha power during walking and the greatest difference to the standing manipulation. The effect of eccentricity indicates that during later visual processing stages, the visual input in the foveal area is less processed than in peripheral areas while walking. That the spatial distribution of attention (or preferred input processing) is different during movement has already been indicated by our previous work, showing that the spatial distribution of visual input processing, as can be modulated via spatial attention, is shifted towards the periphery while walking (Cao & Händel, 2019). In addition, the present study showed that for the central foveal area, there is a large difference in alpha power modulation dependent on the presence of a distractor. Distractor presence will increase the amount of visual input (2 stimuli vs. 1 stimulus). However, this is unlikely the explanation as the difference in input did not affect all eccentricities. However, the perceptual trend does not consistently follow the stimulus induced alpha power change. Strong modulation in induced alpha power goes along with better performance when comparing walking vs standing and also the effect of eccentricity (best for 9°) follows the modulation strength (strongest for 9°) but only during walking. During standing this relationship cannot be observed so clearly. Especially the positive influence of distractor absence on d'cannot be found as increased alpha modulation in the data. This finding suggests that alpha power modulation due to stimulus onset cannot be generalized over stimulus features as behavioural predictor.

One might ask whether the visual flow that was visible through the AR glasses attracted attention during walking and thereby introduced the walking related changes. Regarding the VEP, the optic flow was not time locked to stimulus onset and therefore not additive. Additionally, one would not expect the observed increase in amplitude if attention was directed away from the relevant (VEP introducing) stimulus. Changes in alpha power might be introduced by a general change in attention away from the stimulus. However, our previous study has shown, that the alpha reduction during walking is independent from visual input as it persists in complete darkness (Cao et al., 2020). Pre-stimulus alpha power is therefore unlikely introduced by the optic flow but might represent a change in attentional state independent from visual input. The present data further suggested that the pre-stimulus alpha and the stimulus induced alpha power reflect distinct processes as they show no correlation and alpha power shows no significant difference between movement conditions once the fixation dot appeared. Was the walking related decrease in modulation of stimulus induced alpha power caused by the optic flow visible during stimulus presentation? Previous work indeed suggested increased peripheral visual processing (possibly equivalent to a shift of the attentional focus towards the periphery) during walking (Cao & Händel, 2019), which was also accompanied by a decreased alpha power during stimulation. In this previous study, we did not completely avoid optic flow, but could show through a target detection task that attention was not drawn towards the visible motion introduced by walking. We therefore conclude that also in the current study the reduced modulation of stimulus induced alpha power during walking was unlikely introduced by reduced attention towards the stimulus due to optic flow.

4.6 Conclusion

The current study showed that the established amplitude increase in N1 due to walking can be predicted by pre-stimulus alpha power, which is also significantly modulated by movement. We argue that the pre-stimulus alpha power indicates a general state change which is introduced by walking. This state change might be related to the awareness of sensory input but not to the processing of the input features, as no evidence was found that the N1 amplitude was affected by stimulus features like eccentricity which might influence discrimination sensitivity measured with d’. However,the pre-stimulus alpha power and the

amplitude of N1 were related to the RT. We additionally strengthen the interpretation of pre-stimulus alpha as an indicator of internal states by showing a positive effect of time to be present in alpha power (and N1) and the behavioural performance. This further adds to the important observation that a learning processes existed in both movement states Overall, the finding supports the idea of a movement dependent state in visual processing marked by ongoing alpha activity. However, we additionally found that stimulus induced alpha power was affected by walking dependent on stimulus features like distractor presence and eccentricity. Our work therefore indicates two dissociable movement-related influences on sensory processing. One is based on an ongoing reduction in alpha power due to walking which increases early VEPs to sensory input such as N1. The second influence is marked by stimulus induced alpha power which is specific for the central visual field and when no distracting input is present, indicating a visual spatial change during walking. Our study provides novel insights as to the underlying mechanism of movement induced early sensory enhancement in visual processing. We hypothesise that it is a state change related to sensory awareness which, as we show, is clearly dissociable from influences of walking on stimulus induced processes.

4.7 Supplementary material (Study 3)

S8. The ERP results based on the band-pass filter data between [0.1 30] Hz

The choice of high pass filtering is an ongoing topic in ERP analysis. Some previous studies have shown that early ERP components such as C1 and P1 components are sensitive to high pass filtering and therefore use a maximum 0.1 Hz as the high-pass filter cut-off (Acunzo, Mackenzie, & van Rossum, 2012; Tan & Wyble, 2015). However, given the existence of low-frequency noise, it was further recommended to check the distortion induced by a filter by comparing the waveform with and without having applied a filter on the raw data rather than absolutely specify a 0.1 cut-off value (Acunzo et al., 2012; Maess, Schroger, & Widmann, 2016).

Since the current datasets were contaminated by comparatively stronger low-frequency noise and leads to not only strong drift for each subject data buts also high variance among participants, the [1 30] Hz was used in the bandpass filter. In order to show that the ERP results based on the band pass-filtering at [1 30] Hz is not distorted by the high pass filtering to be a reliable true signal. The main ERP analysis and corresponding results (based on the median value among all participants) from the band pass-filtered data at [0.1 30] Hz are presented below. The artefact rejection procedure is as same as the band pass-filtered data at [1 30] Hz. First, trials were visually inspected using the fieldtrip function ft_rejectvisual, and trials with excessive noise were manually excluded based on the variance within each channel. Second, the principal component analysis was performed to reduce the spatial dimensionality of the EEG data, which was followed by an ICA applied to correct eye movements, heartbeat, and muscle-related artefacts. An average of 3.87 (*SD* = 2.13) out of 16 artefact components were excluded. An average of 17.87 trials (*SD* = 10.60) out of the total 1152 trials were rejected. The following ERP results were based on the polynomial trend corrected by using the *detrend* function in Matlab. The time window of the N1 and P3 components were chosen via visual inspection of the band-pass filter data between [0.1 30] Hz.

Enhanced N1 response during walking

The amplitude of N1 component was averaged over occipital electrodes (i.e. O1, O2, P7 and P8). Based on visual inspection, the N1 component was identified between ([170 220] ms), and the P3 component was between ([250 300] ms). A four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with distractor vs. without distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA with the N1 amplitude showed a significant main effect of movement state ($F(1,24) = 21.27$, $p < 0.001$) (Figure ***S8-1,a-c***). The N1 component was larger during walking ($M = -6.00$, $SD = 4.02$) than during standing ($M = -3.92$; $SD = 3.83$). The main effect of distractor presence was also significant ($F(1, 24) = 7.00$, $p = 0.01$). A stronger N1 was found during "with distractor" manipulation ($M = -5.14$; $SD = 3.70$) than during "no distractor" manipulation ($M = -4.78$; $SD = 3.84$). No other main effects or interaction effects were found statistically significant. To be noted, the N1 enhancement during walking did not interact with any stimulus-related manipulation, including the interaction between movement state and target location ($F(1,24) = 0.45$, $p = 0.51$), the interaction between movement state and distractor presence ($F(1,24) = 1.11$, $p = 0.30$) as well as the interaction between movement state and eccentricity ($F(1,24) = 0.30$, $p = 0.68$). In summary, we find an enhanced N1 response due to walking and due to distractor presence. Importantly, no evidence was found supporting that the effect of movement on N1 enhancement was independent of any external stimulus-related manipulation (target location, distractor presence, and eccentricity).

Reduced P3 response during walking

The posterior P3 component was also tested as to its modulation by movement state, target location, distractor presence, and eccentricity. A four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with distractor vs. without distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA with the P3 amplitude ([250 300] ms) showed only a significant main effect of movement state ($F(1,24) = 17.89$, $p = 0.002$). The P3 component was larger during standing ($M = 0.45$, $SD = 4.65$) than during walking ($M = -1.18$; $SD = 4.07$) (Figure ***S8-1, a-c***). No other effects were significant. Similar to the N1 component, the decreased P3 component during walking did not show any evidence that it was interacted with stimulus-related manipulation, including the interaction between movement state and target location ($F(1,24) = 0.17$, $p = 0.68$), between movement state and

distractor presence ($F(1,24) = 0.04$, $p = 0.85$), and between movement state and eccentricity ($F(2,48) = 0.50$, $p = 0.54$).

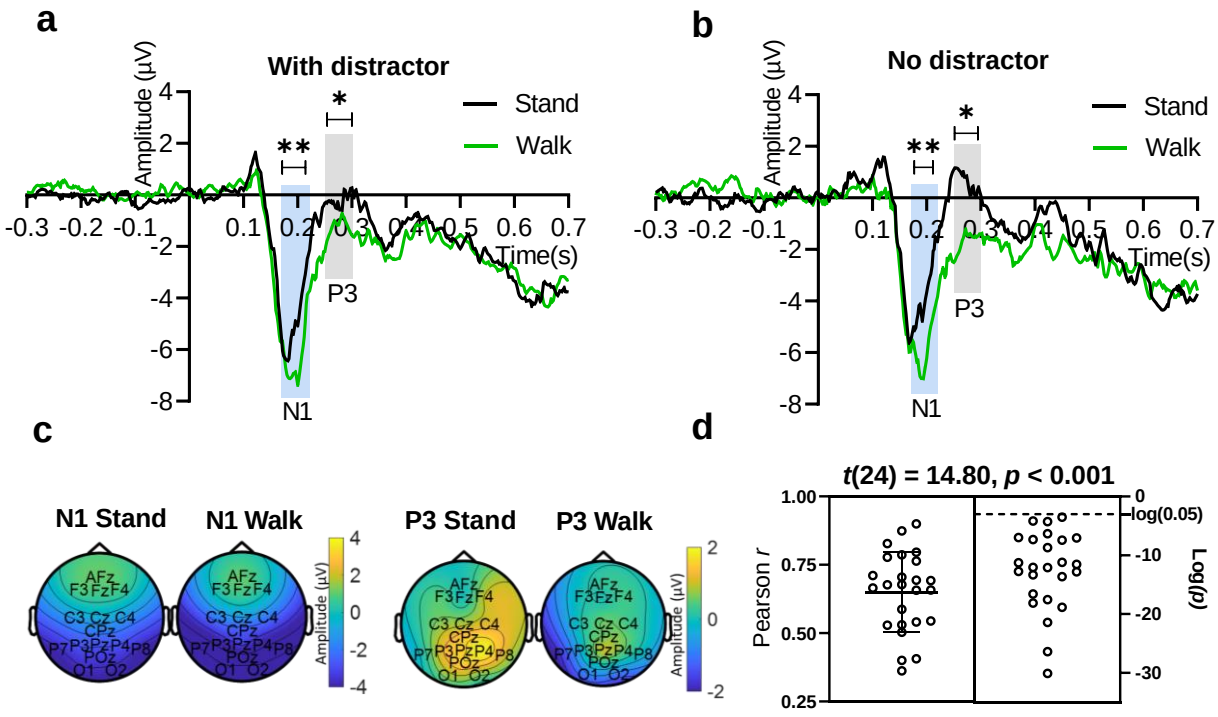

Figure S8-1. N1 enhancement and P3 decrease during walking. The grand average ERP during standing (black line) and during walking (green line) for (***a***) with distractor manipulation and (***b***) no distractor manipulation. Data are presented as mean ± SEM (standard error of the mean).(***c***) The average topography of the N1 ([170 220] ms) and P3 component ([240 300] ms) for standing and walking separately. (***d***) Within each participant (n = 25), the correlation between the N1 and the P3 component was tested based on the average amplitude of 32 trials in each manipulation (n = 36). A significant one-sample t-test between the Pearson r value (Z-transformed) and 0 (n = 25) indicates a positive correlation between N1 and P3 components. Pearson *r* data corresponds to the left y-axis while the *p*-value was plotted on a log scale corresponding to the right y-axis. Each circle represents a participant.

The enhanced N1 component and decreased P3 component during walking were both independent of external stimulus-related manipulations, indicating that the two movement state-related effects may have a common origin. To this end, we checked whether the two components were correlated. The within-participant test based on manipulations showed a

significant positive correlation between N1 and P3 component (one-sample t-test between each participant's *r* value and zero: $t(24) = 14.80$, $p < 0.001$) (Figure ***S8-1,d***).

Pre-stimulus alpha power was reduced during walking and linked to reaction time, N1 and P3 components.

To check whether the N1 and P3 changes induced by walking were driven by an internal movement-induced state change, we compared the pre-stimulus ([1000 1200] ms) and fixation ([-200 0] ms) alpha power (average between [7 -14] Hz) between standing and walking. Alpha power was taken from the same electrodes (P7, P8, O1 and O2) as chosen for the ERPs and the relationship with ERP responses was also analysed. For pre-stimulus alpha power, the results showed a decrease in alpha power band during walking ($M = 17.62$, $SD = 12.01$) compared to standing ($M = 24.37$, $SD = 21.39$) ($t(25) = 3.21$, $p = 0.004$) (Figure ***S8-2,a***). The topography of the pre-stimulus alpha power showed a difference between standing and walking over posterior-occipital electrodes (Figure ***S8-2,b***). We then checked whether the pre-stimulus alpha power is linked to behavioural responses. The within-participants correlation showed a significant correlation between pre-stimulus alpha power and the reaction time (one-sample t-test between each participant's *r* value and zero: $t(24) = -3.32$, $p = 0.002$), with stronger pre-stimulus alpha power linked to a faster response (Figure ***S8-2,d***). The same comparison between standing and walking was performed for alpha power during the fixation time window ([-200 0] ms). However, the fixation alpha power neither differed significantly between standing and walking ($t(24) = -0.58$, $p = 0.57$) (Figure ***S8-2,c***), nor was it correlated with the reaction time (one-sample t-test between each participant's *r* value and zero: $t(24) = -1.05$, $p = 0.31$).

We further checked whether the movement state-related decrease in pre-stimulus alpha power could predict the N1 and P3 component. The correlation between the pre-stimulus alpha power and next trial's N1 and P3 components were first examined (average between standing and walking). As a result, the pre-stimulus alpha power significantly predicted the N1 component (t-test between each participant's *r* value and zero: $t(24) = 2.19$, $p = 0.04$) and the P3 component ($t(24) = 2.43$, $p = 0.02$) (Figure ***S8-2, e, f***).

There was no indication that fixation alpha power was correlated with the N1 component (one-sample t-test between each participant's *r* value and zero: $t(24) = 1.13$, $p = 0.27$) and the P3 component ($t(24) = 0.89$, $p = 0.40$).

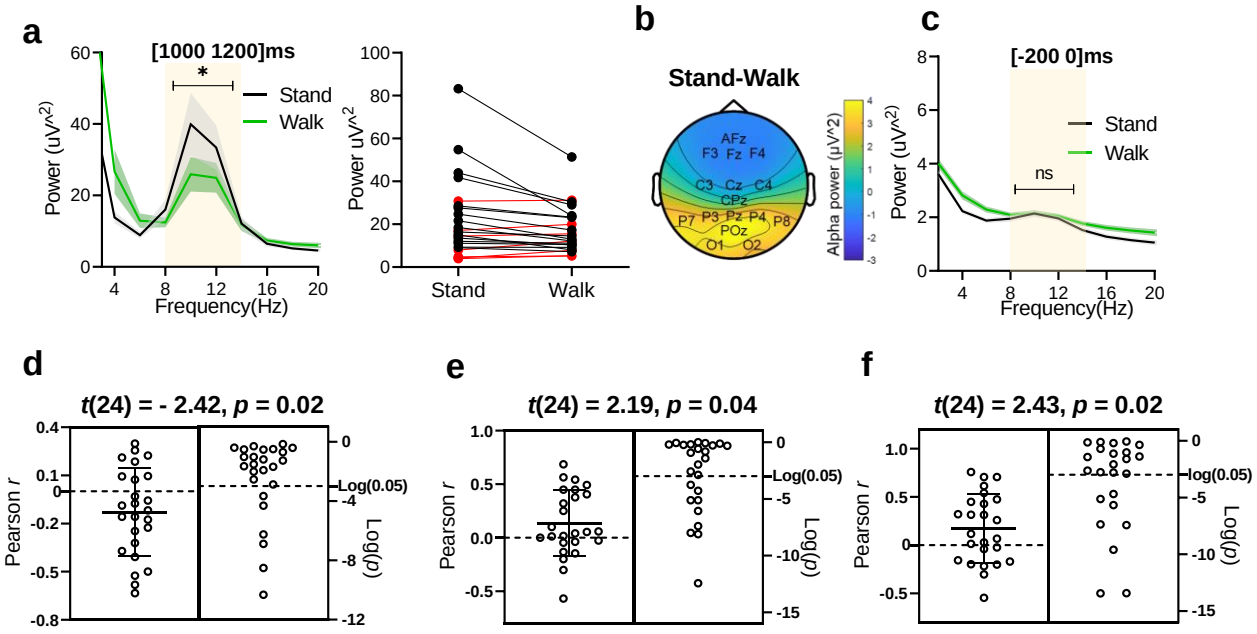

Figure S8-2. Pre-stimulus alpha power predicted the N1 and P3 component and correlated with reaction time. (***a***) EEG power spectra of the non-baseline corrected pre-stimulus time window ([1000 1200] ms) for standing (black line) and walking (green line). Data are presented as mean ± SEM (standard error of the mean) (left panel). Alpha power (average between [8 -14] Hz) during walking was significantly decreased compared to standing (right panel). (***b***) The topography of the difference between standing and walking (stand-walk) during the pre-stimulus time window ([1000 1200] ms). (***c***) EEG power spectra of the fixation time window ([-200 0] ms) for standing (black line) and walking (green line). (***d***) Within each participant (n = 25), the correlation between the pre-stimulus alpha power and the reaction time was tested among all 36 manipulations based on the average amplitude of 32 trials in each manipulations (n = 36). A significant one-sample t-test between the r value (z-transformed) and 0 (n = 25) indicates a prevalent negative correlation between pre-stimulus alpha power and reaction time. The original Pearson r data corresponds to the left y axis while the p values (log scale) correspond to the right y axis. (***e***) Same as in d but between pre-stimulus alpha power and the N1 component. (***f***) Same as in d but between pre-stimulus alpha power and the P3 component.

To summarize, the data band-pass filtered at [0.1 30] Hz also showed that the pre-stimulus alpha power significantly differed between standing and walking and predicted the N1 and P3 components as well as reaction times during both standing and walking.

S9. The EEG results with data filtered between [1 100] Hz and with artefact subspace reconstruction before ICA

Artefact subspace reconstruction (ASR) is a good method for signal correction before the ICA. To further convince the reader of the quality of our data and corresponding analyses, we re-analysed our whole datasets by using a different cut-off of low pass filter (100 Hz) and performing ASR before ICA. The ASR was performed by implementing the clean_artifacts function within the clean_rawdata plugin in EEGLAB (parameters: channel criterion = off, burst criterion = 20, window criterion = off; Other parameters are based on the default). Other pre-processing follows the steps described in the manuscript. An average of 8.30 trials (*SD* = 5.31; out of the total 1152 trials) and 4.27 artefact components (*SD* = 2.27; out of the total 16 components) were rejected. The summary of the main results can be seen in Figure ***S9***.

Walking led to an early internal-state-related processing change

Enhanced N1 response during walking

The amplitude of N1 component was averaged over occipital electrodes (O1, O2, P7 and P8). A four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with distractor vs. no distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA with the N1 amplitude ([170 220] ms) showed a significant main effect of movement state ($F(1,24) = 11.64$, $p = 0.002$) (Figure ***S9a***). The N1 component was larger during walking (*M* = - 4.42, *SD* = 3.20) than during standing (*M* = -3.41; *SD* = 3.13). The main effect of distractor presence was also significant ($F(1, 24) = 4.69$, $p = 0.04$). A stronger N1 was found during with distractor manipulation (*M* = - 4.01; *SD* = 3.15) than during no distractor manipulation (*M* = -3.81; *SD* = 3.02). No other main effects or interaction effects were found statistically significant.

The posterior P3 component was also tested as to its modulation by movement state, target location, distractor presence, and eccentricity. A four-way (movement state: standing

vs. walking; target location: left vs. right; distractor presence: with distractor vs. no distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA with the P3 amplitude ([250 310] ms) showed only a significant main effect of movement state ($F(1,24) = 7.17$, $p = 0.01$). The P3 component was larger during standing ($M = 1.41$, $SD = 2.59$) than during walking ($M = 0.77$; $SD = 2.30$). No other effects were significant.

The enhanced N1 component and decreased P3 component during walking were both independent of external stimulus-related manipulations, indicating that the two movement state-related effects may have a common origin. To this end, we checked whether the two components were correlated. The within-participant test based on manipulations showed a significant positive correlation between N1 and P3 components (one-sample t-test between each participant's *r* value and zero: $t(24) = 2.82$, $p = 0.01$).

Pre-stimulus alpha power was reduced during walking and linked to reaction time, N1 and P3 components.

To check whether the N1 and P3 changes induced by walking were driven by a general movement-induced state change, we compared the non-baseline corrected pre-stimulus ([1000 1200] ms) and fixation ([-200 0] ms) alpha power (average between [8-14] Hz) between standing and walking. Alpha power was taken from the same electrodes (P7, P8, O1 and O2) as chosen for the VEPs and the relationship with VEPs was also analysed.

For pre-stimulus alpha power, the results showed a decrease in alpha power during walking ($M = 17.62$, $SD = 12.01$) compared to standing ($M = 24.37$, $SD = 21.39$) ($t(25) = 3.21$, $p = 0.004$) (Figure ***S9b***). When checking whether the pre-stimulus alpha power was linked to behavioural responses, the within-participants correlation analysis showed a significant correlation between pre-stimulus alpha power and the reaction time (one-sample t-test between each participant's *r* value and zero: $t(24) = 3.01$, $p = 0.01$), with stronger pre-stimulus alpha power linked to a faster response. The same comparison between standing and walking was performed for alpha power during the fixation time window ([-200 0] ms). However, the fixation alpha power neither differed significantly between standing and walking ($t(24) = -0.30$, $p = 0.76$) (Figure ***S9c***), nor was correlated with the reaction time ($t(24) = -1.40$, $p = 0.18$). Note that when testing whether the alpha power changes over time, the results showed that

the pre-stimulus alpha power ([1000 1200] ms) increased with time during both standing (r = 0.92, p < 0.001) and walking (r = 0.91, p < 0.001). However, the fixation alpha power ([-200 0] ms) increased with time only during standing (r = 0.79, p < 0.001) but not during walking (r = 0.27, p = 0.13) (Figure ***S9e***).

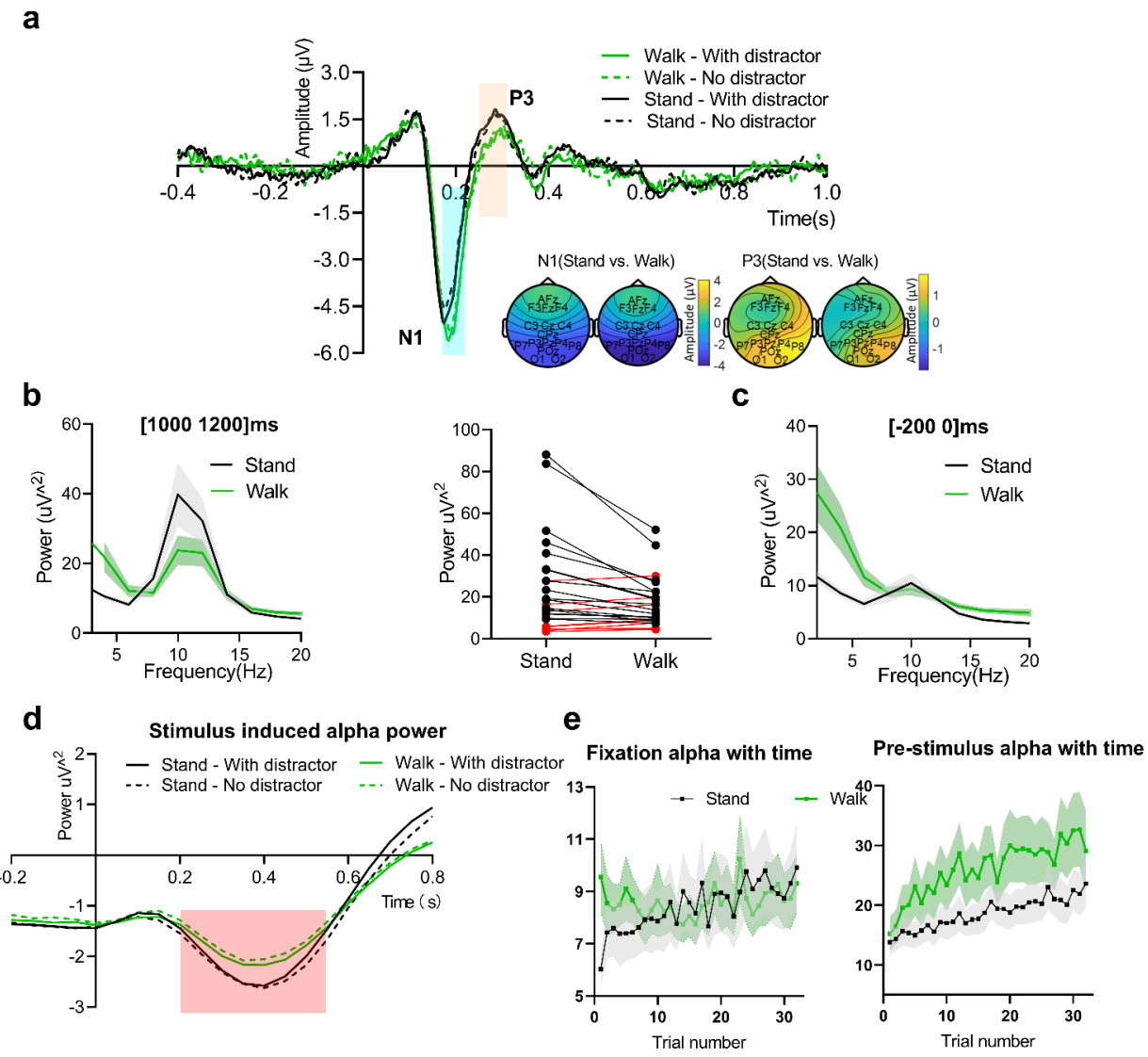

Figure S9. The results with data filter between ([1 100] Hz) and with an ASR pre-processing. (***a***) The N1 component was enhanced and the P3 component was reduced during walking (green) compared to standing (black) "with distract" or (solid line) and "no distractor" manipulation (break line). The difference can also be seen in the topography of the N1 ([170 220] ms) and P3 component ([250 310] ms) for standing and walking separately. (***b***) Pre-stimulus alpha power was reduced during walking. (***c***) No difference in fixation alpha power between standing and walking. (***d***) The stimulus induced alpha power ([200 550] ms) for stand

and walking in “with distractor” and “no distractor” manipulation. (***e***) Pre-stimulus alpha power increased with time during standing and walking (left panel), while fixation alpha power only increased with time during standing (right panel).

We further checked whether the movement state-related decrease in pre-stimulus alpha power could predict the N1 and P3 components. The correlation between the pre-stimulus alpha power and the next trial’s N1 and P3 components was first examined (based on all 36 manipulations). As a result, the pre-stimulus alpha power significantly predicted the N1 component (t-test between each participant’s *r* value with zero: $t(24) = 2.70$, $p = 0.01$) and the P3 component ($t(24) = 3.24$, $p = 0.03$).

Stimulus induced alpha power is less modulated during walking and dependent on distractor presence and eccentricity

Posterior baseline-corrected alpha power was taken from the same electrodes as used for the ERP analysis (P7, P8, O1 and O2). The time window that demonstrated the clearest alpha power difference between standing and walking and after the P3 component time window was identified through visual inspection of an average over all manipulations ([200 550] ms). A four-way (movement state: standing vs. walking; target location: left vs. right; distractor presence: with distractor vs. no distractor; eccentricity: 1.3° vs. 9° vs. 16°) repeated-measures ANOVA with alpha power was performed on the averaged power values in this time window. A significant interaction effect between movement state and distractor presence was observed ($F(1, 24) = 5.22$, $p = 0.03$), showing that the effect of movement was dependent on stimulus features (Figure ***S9d***).

We further investigated whether the stimulus induced alpha power ([200 550] ms) reflected a similar process as the early sensory N1 and P3 amplitude change which was predicted by pre-stimulus alpha power. A within-participant correlation (averaged over trials separately for each manipulation) between stimulus induced alpha power and pre-stimulus alpha power was performed. A one-sample t-test between each participant’s *r* value and zero did not indicate a prevalent correlation ($t(24) = -1.41$, $p = 0.17$) . Additionally, we neither observed an indication for a correlation between stimulus induced alpha and the N1 ($t(24) = -0.40$, $p = 0.70$) nor the P3 component ($t(24) = 0.80$, $p = 0.43$). The stimulus induced alpha

power was not modulated by time during both standing (r = - 0.02, p = 0.91) and walking (r = - 0.10, p = 0.60).

S10. The increase of alpha power from trial 1 to trial 576 in each movement state

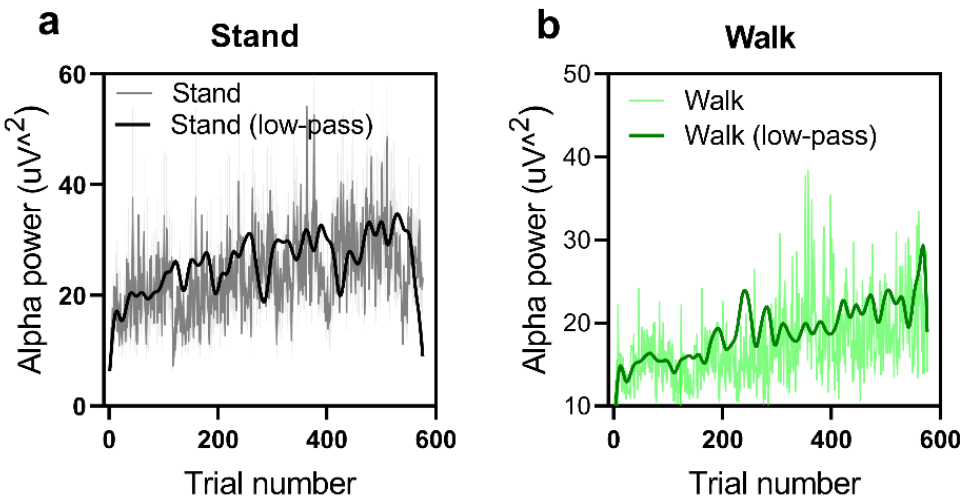

Figure S10. Pre-stimulus alpha power increase with time. The averaged alpha power from trial 1 to trial 576 showed an increase tendency for both standing (***a***) and walking (***b***). Low-pass filtered data at 1Hz demonstrated a clearer trend.

5. Study 4: Walking modulates active auditory sensing

Walking modulates active auditory sensing

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This is an unpublished manuscript.

Abstract:

Walking is a body movement that serves various ecological functions in human daily life. In the current study, we assessed if walking and the walking direction modulates auditory processing and the underlying neuronal responses. To this end, we combined walking in a pre-defined path with a continuous auditory entrainment and measured the auditory steady-state response (ASSR) and other neural markers using mobile EEG. In two experiments, we found increased auditory entrainment (ASSR power) and early auditory evoked responses during walking compared to standing and stepping-in-place. The modulation of ASSR power due to walking was robustly predicted by the modulation of occipital alpha power due to walking. In addition, we found that only peripheral auditory input induced an enhancement of ASSR perturbation during walking, which is consistent with a spatially specific improvement

of sensory processing during walking. Most interestingly, we found that the auditory entrainment was lateralized by the walking path. The stronger entrained side was always in line with the turning direction even so this means that the ASSR lateralisation index had to change with respect to the participant's view. This suggests a possible role of walking-induced neural modulation in active sensing. In general, the current work shows that walking changes auditory processing in a walking path specific way which might serve to optimize navigation. The walking path related modulation might further reflect a shift of attention, marking a higher-order form of active sensing.

Keywords: Auditory steady-state response; Alpha oscillation; Active sensing; Mobile brain imaging; Natural walking; Sensory processing

5.1 Introduction

The ability to move is an essential feature of living organisms. The development of mobile electroencephalography (EEG) has helped to increase our knowledge about how movements of the body interact with cognition and underlying neural processes in humans (De Vos & Debener, 2014; Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Makeig, Gramann, Jung, Sejnowski, & Poizner, 2009). The effects of body movement on cognition range from simple perceptual changes (Bullock, Cecotti, & Giesbrecht, 2015; Cao & Händel, 2019; Cortney Bradford, Lukos, Passaro, Ries, & Ferris, 2019; Yagi, Coburn, Estes, & Arruda, 1999) to higher order processes like learning and creativity (Frith, Ryu, Kang, & Loprinzi, 2019; Lhuillier, Gyselinck, Piolino, & Nicolas, 2021; Wilson & Gibbs, 2007). However, the effects described in literature are rather variable, can be specific for certain cognitive processes and might further be dependent on movement type, intensity, duration and timing (Cantelon & Giles, 2021; Lambourne & Tomporowski, 2010; McMorris & Hale, 2012; Schmidt-Kassow & Kaiser, 2023). As discussed in the review by Schmidt-Kassow and Kaiser (2023), it is crucial to consider the specific movement execution, as well as its ecological relevance when considering the interplay of motor activity and cognition.

In electrophysiology, a robust finding in humans is the reduction of ongoing alpha power in the parieto-occipital cortex during body movement, including free walking, treadmill walking and stationary cycling (Cao, Chen, & Händel, 2020; Ehinger et al., 2014; Kuziek, Redman, Splinter, & Mathewson, 2018; Lin, Wang, Wei, & Jung, 2014; Nenna, Do, Protzak, & Gramann, 2020; Robles et al., 2021; Scanlon, Townsend, Cormier, Kuziek, & Mathewson, 2019; Shaw et al., 2018; Vaughn et al., 2021; Wagner et al., 2019; Zink, Hunyadi, Huffel, & Vos, 2016). This alpha power modulation is most prominent over occipital areas, and has been shown to be independent of impedance, eye movement and visual input, i.e. it persisted in complete darkness (Cao et al., 2020). Additionally, there is a concurrent amplification of early visual (Bullock et al., 2015; Chen, Cao, & Haendel, 2022a, 2022b; Dodwell, Liesefeld, Conci, Muller, & Tollner, 2021) and auditory event related potentials (Scanlon et al., 2019; Vaughn et al., 2021) during body movement. These findings are in line with animal studies showing that the firing rates of neurons in the primary visual cortex are modulated by the running speed. Also this neural modulation persisted if the animals ran in complete darkness (Ayaz,

Saleem, Scholvinck, & Carandini, 2013; Dadarlat & Stryker, 2017; Dipoppa et al., 2018; Kanamori & Mrsic-Flogel, 2022; Kaneko, Fu, & Stryker, 2017; Neske, Nestvogel, Steffan, & McCormick, 2019).

Alpha activity has been associated with neural inhibition (for reviews, see (Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch, Sauseng, & Hanslmayr, 2007a). Accordingly, a movement-induced alpha power decrease could reflect reduced inhibitory activity and therefore lead to the observed enhancement of visual responses. Indeed, the strength of the walking-induced alpha power reduction can predict a concurrent amplification of early visual event related potentials during walking (Chen et al., 2022a). Similarly, Cao and Händel (2019) found a correlation between ongoing alpha oscillations and the walking induced changes in amplitude of an entrained steady state visual evoked potential (SSVEP). Additionally, several findings suggest that locomotion can modulate sensory processing in a spatially specific way. Cao and Händel (2019) showed walking enhanced neural processing of peripheral visual input. This modulation was paralleled by a behavioural effect in a concurrently probed target-detection performance. As the neural modulation was linked to occipital alpha power, they proposed that the increased processing of peripheral visual input during walking was associated with altered inhibitory processes during walking. Also Benjamin, Wailes-Newson, Ma-Wyatt, Baker, and Wade (2018) showed detection/discrimination thresholds to be higher during treadmill walking than a stationary condition when visual stimuli were presented together with a surrounding mask. The stimulus-induced SSVEP contrast modulation in this surround mask was also enhanced during walking. Their results generally indicate that walking leads to improved surround suppression. Another recent study, using a single-stimulus visual detection paradigm, provides further evidence of changed spatial sensory processing (Reiser, Arnau, Rinkenauer, & Wascher, 2022). When looking at the second peak of the components measured at posterior sites contralateral to the presented stimulus (the N1pc/N2pc complex), they found that walking led to a decreased latency compared to stationary states only in the extrafoveal stimulus condition. They interpreted the neural results as an indication of faster re-entrant processing of stimuli that have a diminished saliency during walking.

In summary, there are three interesting observations that can be drawn from the existing literature. First, walking changes occipital alpha power independent of the visual input, and modulated visual but also auditory evoked potentials. This suggests some independence from the visual domain. Second, during walking, visual sensory processing can be changed in a spatially specific way. This could indicate a process that is related to navigation. Third, the walking-induced alpha power reduction can predict the neural response change to visual input. Based on these findings, we proposed that the change of ongoing oscillatory activity and neural sensory responses during walking is part of an optimization strategy to most effectively process sensory input that is relevant during natural movement (Cao & Händel, 2019). Locomotion is usually based on some form of navigation that mainly relies on peripheral visual input (Warren, Kay, Zosh, Duchon, & Sahuc, 2001). However, also auditory input might hold relevant information which informs our path.

We specifically hypothesized for the auditory domain that：

(1) Walking leads to a decrease in alpha power and a concurrent increase in auditory processing.

(2) Particularly peripheral auditory input will be modulated by walking.

(3)The walking path will affect the modulation of neural activity representing auditory processing.

(4) The walking-induced effect on auditory processing is strongest for natural walking.

To test those hypotheses, two experiments were performed. To assess if auditory processing is affected by walking and if the walking direction further modulates this processing, we combined a well-defined walking task with continuous auditory entrainment and mobile EEG. The auditory steady-state response (ASSR) is an electrophysiological measure of brain activity that reflects the entrainment of neural activity to a rhythmic auditory stimulus (Galambos, Makeig, & Talmachoff, 1981; Picton, Dimitrijevic, & John, 2002; Picton, van Roon, & John, 2009). Such an approach allows to assess a purely auditory neural signal, namely the entrained one, despite using a low-density mobile EEG system which might additionally be prone to motion artefacts and noise. The concurrent recording of alpha power

allowed to evaluate the relationship between movement induced alpha power reduction and ASSR power. The first experiment focused only on the steady-state responses whereas the second experiment also investigated a stimulus-induced perturbation of the ASSR inducing stimulus. As the perturbation was either presented in the periphery or centrally, we could assess if particularly peripheral auditory in put was modulated by walking. Additionally, we added a stepping-in-place condition in experiment 2 to understand if natural walking is most effective for the observed neural changes.

The results revealed an enhanced ASSR power during walking compared to standing (experiment 1 and experiment 2) and compared to stepping (experiment 2). The modulation of ASSR power due to walking was also robustly predicted by the modulation of occipital alpha power due to walking (experiment 1 and experiment 2). Those findings support hypotheses 1 and 4. Further, we found that only peripheral auditory ASSR perturbation induced an enhancement of ASSR perturbation during walking (experiment 2), which is consistent with the hypothesized improvement of peripheral processing (hypothesis 2). Additionally, we found that the side of stronger entrainment, marked by an ASSR lateralisation index, was modulated by the walking path (experiment 1 and experiment 2), which supports our hypothesis 3. However, we did not find any evidence that the effect of the ASSR perturbation was dependent on the walking path.

5.2 Materials and Methods

5.2.1 Participants

35 participants recruited from a local participants pool via the SONA system (21 females, age: 28.05 years (SD = 3.51) took part in the study. 34 participants completed both experiment 1 and experiment 2. One participant withdrew from the study shortly after experiment 2 began, therefore only data from experiment 1 was collected. All participants reported having normal bilateral hearing. They gave their written informed consent prior to the participation and received a payment of 10 euros per hour for their participation. The study was approved by the local ethics committee and complied with the European data protection law (DSGVO).

5.2.2 Experimental design

The study included 2 experiments. The first experiment focused on the ASSR and the second experiment aimed to also investigate the stimulus induced perturbation of the ASSR amplitude. Both experiments were performed in a spacious room measuring approximately 5*6 meters. All auditory stimuli were generated using PsychPortAudio software on a Dell laptop (model: Latitude E7440) and were presented through in-ear earphones (AirPods, Model: A1602).

Experiment 1

Each participant completed two testing blocks, each containing a stepping, a walking, and a standing condition. Half of the participants performed the three movements with an order of stepping – walking – standing, and another half of the participants with an order of standing – walking – stepping. During the standing condition, participants were instructed to stand in the centre of the marked walking pathway (Figure ***16a***, green dot). For the stepping condition, participants were asked to walk on the spot in the same location where they executed the standing condition (Figure ***16a***, green dot). During the walking condition, participants were asked to walk in an "8" shaped pathway. The dimensions of the walking pathway can be seen in Figure 16a, left panel. Specifically, the walking path included walking straight (heading to left/right, indicated by dashed yellow arrows), making a semi-circular left turn, and making a semi-circular right turn. The walking path was indicated by arrows attached to the ground, but participants did not need to attend to the exact walking path (the black 8 path in the figure is for illustration purposes only and was not presented in the actual experiment). Note that the starting location (Figure ***16b***, orange dots) for walking was balanced among participants to control for external variables, such as the location of the light source and the visual input provided by the arrow. Figure ***16a*** walking path 1 illustrates the experimental conditions for participants who first started by walking straight to the left and then turned right. The other half of the participants began by walking straight to the right and then turned left, and accordingly, all yellow arrows were also flipped to align with this condition's walking instruction, as indicated by Figure ***16a*** walking path 2. The walking speed was trained before the start of the experiment to ensure that participants took approximately 12 seconds (6s for each left/right turn) to complete one full "8" shaped pathway. The

experimenter also visually monitored the speed throughout the testing sessions. The testing duration of stepping, walking and standing was 120s, 480s and 120s. The total testing time for each block was ~12min.

During the 3 movement conditions, participants were exposed to a continuous stream of sinusoidal amplitude-modulated tones to elicit an auditory steady-state response (ASSR). The tones were modulated at frequencies of 39 Hz and 41 Hz, separately for the left and right auditory input (presented to the left and right ear, respectively) (Figure ***16b***). We chose these two frequencies as ASSR power was found to reach a maximum response around 40 Hz in humans (Galambos et al., 1981; van der Reijden, Mens, & Snik, 2001). The carrier frequency was set to 1000 Hz, with a modulation depth of 100%. To avoid sudden onsets and offsets of the signal, the modulating signal was windowed with a ramping function. The auditory stimuli had a sampling rate of 44100 Hz.

Experiment 2

Each participant completed four testing blocks, each containing a walking and a standing condition. The standing and walking tasks were the same as in experiment 1. The total testing duration for the walking condition was approximately 8 minutes for each block. The first half of the participants began with the standing condition, while the other half began with the walking condition. The starting point (1 or 2 in Figure ***16a***) of walking was again balanced among participants to control for possibly confounding external variables.

Participants were exposed to a continuous stream of sinusoidal tones, which were amplitude-modulated at either 39 and 41 Hz for the left and right ear input just as described for experiment 1. To perturb the auditory stimuli, burst tones lasting 100 ms were intermittently presented in both ears (the central perturbation condition), the left ear or the right ear (the peripheral perturbation condition) at unpredictable latencies and order (Figure 16***b***). When the perturbation occurred in the central position, both the 39 Hz and 41 Hz tones were interrupted, and participants reported hearing a burst tone in the frontal midline. When the perturbation occurred in the left ear, the 39 Hz tone was interrupted, and when it occurred in the right ear, the 41 Hz tone was interrupted. Participants in this case reported hearing a burst tone in a left or right location, respectively. During the standing condition,

participants experienced 8 perturbations at intervals of 3 -7s for each position (central, left, or right). The total testing duration for each standing block was approximately 2 minutes. During the walking condition, participants experienced 32 perturbations also every 3-7 s at each position (central, left, or right) to ensure that enough trials of perturbation could be recorded during turning left and right.

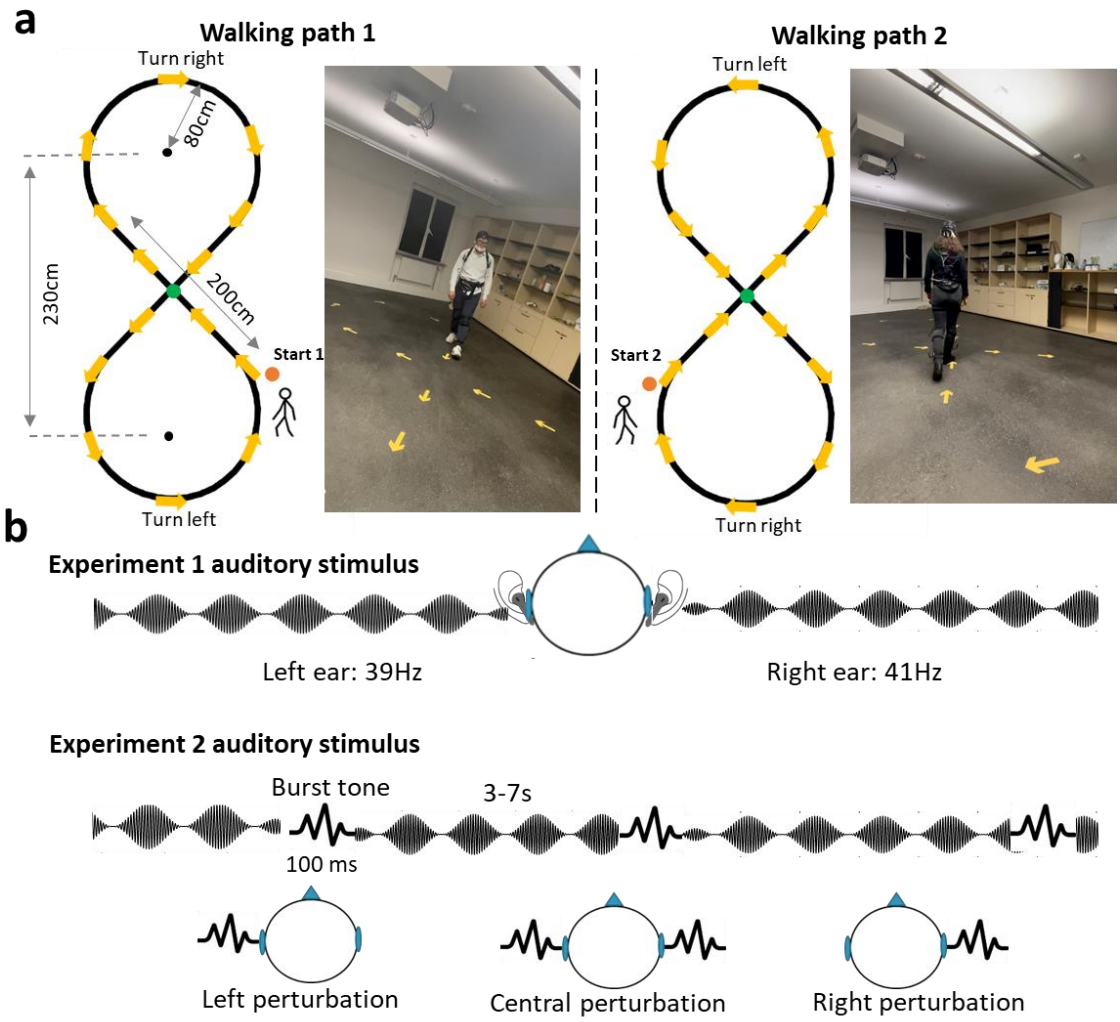

Figure 16. The experimental set-ups. (***a***) Movement Task: In experiment 1, participants engaged in three movement conditions: stepping, standing, and walking. In experiment 2, participants performed two movement conditions: standing and walking. During the standing condition, participants were instructed to stand in the centre of the marked walking pathway (indicated by a green dot). For the stepping condition, participants were asked to walk on the spot in the same location as the standing condition. For the walking condition, participants walked in an '8' shaped walking path. The start location is marked with an orange dot. Half of

the participants walked on path 1, starting with a rightward turn and then a leftward turn. For the other half of the participants, the order of turn direction was reversed (path 2). The two walking paths were indicated by yellow arrows attached to the ground (the black '8' path in the figure is for illustration purposes only and was not presented in the actual experiment). (***b***) The auditory stimuli: In experiment 1, participants listened to tones that were modulated at frequencies of 39 Hz and 41 Hz for the left and right ear, respectively. In experiment 2, in addition to the consistently played tones, intermittent burst tones (perturbations) lasting 100 ms were presented. Perturbations could occurr simultanously in both the 39 Hz and 41 Hz tones, and participants reported hearing it in a midline location, hence we termed it central pertubation. The perturbation could also occurred only in the left ear, i.e. the 39 Hz tone was interrupted, or in the right ear, i.e. the 41 Hz tone was interrupted. The interruption was then perceived either in the left or right periphery.

5.2.3 Data Acquisition

EEG data were recorded using the Smarting mobile EEG system (mBrainTrain LLC, Serbia). The EEG system has 24 recording electrodes with a sampling rate of 500 Hz. Among the 24 electrodes, 18 electrodes were used for EEG recording (with one electrode on each earlobe for possible re-referencing). Another 6 electrodes, which were placed around the eyes (3 electrodes for each eye: one above and one below the eyes, one near the outer canthus), were used for electrooculogram (EOG) recording. The EEG signal amplifier and data transmitter have wireless data transmission via Bluetooth.

Motion data was recorded (velocity and acceleration; sampling rate: 120Hz) with a Perception Neuron system (https://neuronmocap.com/products/perception_neuron; Noitom Ltd., China). Three-dimension velocity and three-dimension acceleration data were collected from three sensors: one attached to each ankle (a few centimetres above the lateral malleolus) and the third one attached to the participant's back (at the waist level). Data transmission was also achieved via Bluetooth.

The software Lab Streaming Layer (https://github.com/sccn/labstreaminglayer) was used to collect and synchronize all data streams (event markers, EEG and motion data).

Stimulus generation and presentation were coded in MATLAB (The Mathworks Inc, R2019b) using the Psychtoolbox (Kleiner, Brainard, & Pelli, 2007).

5.3 Data analysis

5.3.1 Pre-processing

The EEG data analysis was performed using the Fieldtrip toolbox (Oostenveld et al., 2011) and custom scripts developed in Matlab (The MathWorks Inc., USA). For both experiments, we excluded two participants' data due to data transmission errors of the motion data. Additional 3 datasets recorded in experiment 1 and 4 datasets recorded in experiment 2 were excluded because of the failure to elicit an auditory steady-state response (ASSR) with a clear frequency peak power at either 39 Hz or 41 Hz. After these exclusions, data from 30 participants were included in the final analysis of experiment 1, and 28 participants were included in the final analysis of experiment 2.

EEG data from each participant was first re-referenced to the average of two earlobe electrodes. The data was then high-pass filtered at 1 Hz and low-pass filtered at 100 Hz. A band-stop filter between 49.5 Hz and 50.5 Hz was applied to remove 50 Hz line noise. The data was then reduced to 16 dimensions using principal component analysis (PCA), followed by independent component analysis (ICA) using the "runica" (Infomax) approach. The power spectrum of each ICA component was obtained using Welch's method with a 1 s time window, 50% overlap, and 1 Hz resolution.

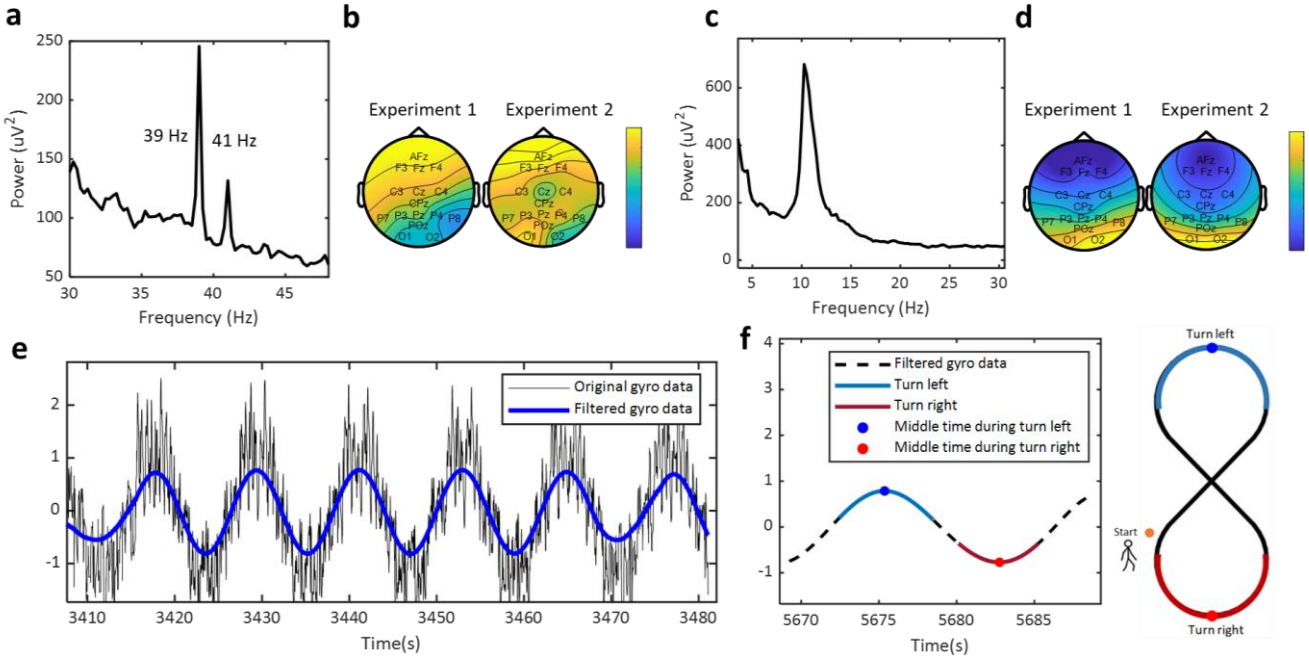

Figure 17. Data pre-processing. (***a***) Referenced and filtered EEG data were subjected to independent component analysis. The ICA component with the highest ASSR was selected for further analysis. An example component is shown. (***b***) The topography of all selected components averaged across all participants are shown for experiment 1 and experiment 2. The plots show the ICA weights, which represent the relative projections of the corresponding component to each electrode. The colour in the topographic plot represents the strength or magnitude of the weights at each electrode. (***c-d***) Example alpha component and the topography of all alpha component averaged across all participants separately for experiment 1 and experiment 2. (***e***) Example period of raw (black line) and low-pass filtered gyroscope data (blue line). (***f***) the periods corresponding to turning left (blue areas) and turning right (red areas) are extracted based on the low-pass filtered gyroscope data. The peak of the sine wave, representing the middle time point during the actual turning path, was defined as the 0 time point (marked with a blue and red dot, respectively) and used for the later analysis of ASSR lateralisation dependent on the turning direction.

The component(s) with the strongest ASSR signal, with respect to the 39 and 41 Hz spectral power, was (were) selected for further analysis. An example component can be seen in Figure ***17a***. Note that we did not have specific requirements regarding the topography distribution when selecting the ASSR component(s). On average, 1.67 (SD = 0.66) ASSR components were obtained per participant in experiment 1 and 1.89 (SD = 0.88) ASSR

components were obtained per participant in experiment 2. The average topography of the components selected between all participants can be seen in Figure ***17b*** for the two experiments. In general, the frontal electrodes had the largest weights of the ASSR components. For the selection of the alpha component, the criteria from our previous study were used (Cao et al., 2020). 1. A local peak from 6 to 14 Hz in the component's power spectrum needs to be visible; 2. The width of the local peak, which was defined as the frequency width between the two adjacent local minimums, should be at least 4Hz (avoiding noisy transient peaks). If there was more than one local peak, the local peak with the largest width was taken (also for step 3). 3. The power at the local peak frequency should be at least 3 times higher than the mean power between 20 and 50Hz (avoiding components with a broadband high power); 4. In the ICA topography, the maximum absolute weight from sensors in the occipital area (O1, O2, and POz) should be larger than the maximum absolute weight from all other sensors. Following these selection criteria, 8 participants were excluded as no components fulfilled the above requirements in experiment 1 and 5 participants were excluded in experiment 2. On average, with participants who fulfilled the criteria, 1.47 (*SD* = 1.07) alpha components were obtained per participant in experiment 1 and 1.83 (SD = 0.78) components were obtained per participant in experiment 2. An example alpha component can be seen in Figure ***17c***. The topography of the components selected and averaged over all participants can be seen in Figure ***17d*** for the two experiments.

5.3.2 The walking path extraction (both experiment 1 and 2)

The walking path was extracted in both experiment 1 and experiment 2, using the same procedure based on the gyroscope data recorded during walking. For each left and turn right, the 0 time point was defined as the peak in the low-pass filtered gyroscope data (Figure ***17e***). This corresponds to the middle time point during the turn (Figure ***17f***, marked with a blue dot for left turn and red dot for right turn). The average number of left turns for each participant was 33.92 (SD = 6.61), and the number of right turns was 37.05 (SD = 5.52). The duration of left turns was on average 6.41 seconds (SD = 0.968), and the duration of right turns was on average 6.43 seconds (SD = 0.973). A turn trial was then defined as the time window of 0 time point ± 2 seconds, resulting in a 4-second trial.

5.3.3 The ASSR and alpha power analyses (both experiment 1 and 2)

We first compared the overall ASSR power in experiment 1 between the three movement states (standing vs. walking vs. stepping). To this end, for each movement state, the pre-processed EEG data based on the identified ASSR component(s) was cut into 1s periods with a 50% overlap in time. In order to minimize the influence of aperiodic noise on the ASSR power, we parameterized the aperiodic component using the python FOOOF-Toolbox23 (Donoghue et al., 2020). The toolbox assumes that aperiodic 1/f activity can be separated from the periodic proportion (defined as power over and above broadband 1/f-activity) of the power spectrum. This method has been applied in many mobile EEG studies (Canessa, Palmisano, Isaias, & Mazzoni, 2020; Protzak & Gramann, 2021). Individual power values were parameterized as the power of the identified peaks between 1 - 48 Hz. With the parameterized power, a two-way (movement state: step vs. stand vs. walk; perturbation location; central vs. peripheral (left vs. right; ASSR frequency; 39 Hz vs. 41 Hz) repeated-measures ANOVA was performed with the mean parametrized ASSR power. Throughout the manuscript, the two lateral frontal electrodes (F3 and F4) were selected. The comparison in experiment 2 focused on the walking and standing conditions. We conducted t-tests separately for the two ASSR frequencies (39 Hz and 41 Hz) between standing and walking.

Furthermore, we examined whether walking led to a decrease in alpha power, as reported in previous studies. The parameterized power was obtained using the same method as for the ASSR power but was based on the identified alpha components. We compared the average alpha power ([8 14] Hz) from the two occipital electrodes (O1 and O2) using paired-sample t-tests between different movement states in both experiments. Throughout the results in the manuscript, the alpha power and ASSR power always refer to the parameterized power.

5.3.4 The ASSR lateralisation analyses

The time resolved ASSR amplitude was obtained through a Hilbert transformation of the band-pass (+- 0.5 Hz of the frequency of interest) filtered data on each 4 s epoch. An ASSR lateralisation index (ASSR LI) was then computed which indexed the lateralisation of entrainment for each time point:

ASSR lateralisation index:

$$\frac{\text{(39Hz ASSR amplitude – 41Hz ASSR amplitude)}}{\text{abs(39Hz ASSR amplitude) + abs(41Hz ASSR amplitude)}}$$

Since the 39 Hz ASSR tone was consistently presented to the left ear, while the 41 Hz tone was consistently presented to the right ear, the ASSR amplitude at 39 Hz would reflect the strength and synchrony of the neural activity in response to left side input, while the ASSR amplitude at 41 Hz would reflect the strength and synchrony of the neural activity in response to right side input. Therefore, a positive ASSR modulation index indicates a stronger processing to the left side while a negative ASSR modulation index indicates a stronger processing to the right side with respect to the midline of the head, i.e. between the two ears. The ASSR modulation index was computed for each time point.

To check whether the ASSR modulation index was influenced by the turning direction, a cluster-based permutation statistical method was used to assess if the amplitude difference between left turn and right turn was significantly different) (Maris & Oostenveld, 2007). The data were shuffled (1,000 permutations) to estimate a 'null' distribution of the effect size based on cluster-level statistics (cluster-defining threshold: $p < 0.05$). Significance of the t-value of the original test is assumed if the t-value falls above the upper 5% of permeation t-values. The time window of the statistical comparison was between [-2 2] s.

5.3.5 The ASSR perturbation analyses (experiment 2 only)

The modulation of ASSR perturbation by movement condition

To investigate how the sensory-specific sensory processing was modulated by movement and perturbation location, we compared the amplitude of the burst tone-evoked ASSR perturbation. The onset time of the burst tone was extracted based on event markers and defined as the 0 time point. A perturbation trial was defined as the time window of 0 time point ± 2 seconds, resulting in a 4-second trial.

As described above, a time-resolved ASSR amplitude was obtained through a Hilbert transformation of the band-pass (+- 0.5 Hz of the frequency of interest) filtered data on each 4 s epoch. Then the burst tone evoked ASSR perturbation was calculated after averaging over all trials in each condition. A baseline correction was applied to a pre-time window ([-500 0]

ms) with log transformation. The strength of the ASSR perturbation was calculated as the average amplitude between ([0 700]) ms after the burst tone onset between all trials. A 3-way (movement state: stand vs. walk; perturbation location; left vs. right vs. central; ASSR frequency; 39 Hz vs. 41 Hz) repeated-measures ANOVA was performed with the mean ASSR amplitude perturbation. Throughout the manuscript, we used a Greenhouse-Geisser correction for ANOVA results when necessary, and statistical significance was defined as $p < 0.05$.

The modulation of ASSR perturbation by walking path direction

The onset of the burst tone was further classified based on the direction of turning during which it occurred, i.e. bursts that occurred while turning left and bursts that occurred while turning right. A 3-way (turn direction: left vs. right; perturbation location; left vs. right vs. central; ASSR frequency; 39Hz vs. 41Hz) repeated-measures ANOVA was performed with the mean ASSR amplitude perturbation from the two lateralised frontal electrodes amplitude (F3, F4) during ([0 700] ms) after the burst tone onset.

5.3.6 ERP analyses (experiment 2 only)

To check the auditory evoked response induced by the burst tone, the filtered data were epoched into trials with time window of ± 2 seconds around the burst tone. The EEG data were baseline-corrected by applying a 700 ms pre-stimulus (averaged over ([-700 0]) ms) absolute baseline to each trial. The grand average ERP was calculated using the again electrodes F3 and F4. We compared the first and second positive component (named as P1 and P2 component). The time windows of the P1 and P2 components were selected by using a 50 ms window centring the positive peaks. In this ERP analysis, a 2-way (movement state: stand vs. walk; perturbation location: left vs. right vs. central) ANOVA was performed with the P1 and P2 component amplitude separately.

5.3.7 Correlational analysis

To investigate the potential correlation between modulation of alpha power due to walking and the neural markers of sensory processing, correlational analyses were performed. Except for the exploratory test for the evoked P2 component, all correlations

were one-sided and based on our hypotheses. We utilized the Spearman correlation coefficient for these analyses. Outlier rejection was conducted using the method from the Robust Correlation Toolbox (Pernet, Wilcox, & Rousselet, 2013).

Frequency analysis: first, correlation analysis was performed between the alpha power modulation and the ASSR power modulation due to walking, averaging between the two frequencies (39 Hz and 41 Hz). This aimed to assess the relationship between alpha power and ASSR power modulation due to walking. Additionally, we examined the relationship between the alpha power modulation and the ASSR amplitude perturbation modulation due to walking, again averaging between the two frequencies (39 and 41 Hz). This analysis aimed to investigate whether alpha power modulation is associated with ASSR perturbation modulation due to walking.

ERP analysis: The relationship between the modulation of early burst tone evoked response (P1), and modulation of the alpha power was examined. Additionally, the correlation between the modulations of the P1 component amplitude and ASSR power was also calculated. The relationship between the modulations P2 component and ASSR perturbations was additionally assessed to determine whether the P2 component marks similar processes as those indicated by ASSR perturbations that was modulated by walking.

5.4 Results

5.4.1 Enhanced ASSR power was related to the decreased alpha power during walking

We first compared the overall ASSRs power between the three movement states in experiment 1. The two-way (movement state: step vs. stand vs. walk; ASSR frequency; 39 Hz vs. 41 Hz) repeated-measures ANOVA was performed with the ASSR power averaged of the two frontal lateral electrodes (F3, F4). The results showed a main effect of movement (F(2, 58) = 7.54, p = 0.01), with the ASSR power during walking (M = 0.31, SD= 0.51) being higher than during stepping (M = 0.15, SD = 0.23) (post-hoc t(29) = - 2.37, p = 0.02) and during standing (M = 0.07, SD = 0.10) (post-hoc t(29) = - 2.80, p = 0.01) (Figure ***18a***). The higher ASSR power during stepping than standing also reached significance (post-hoc $\underline{t}$(29) = -2.37, p = 0.02). The main effect of ASSR frequency was also significant (F(1, 29) = 4.56, p = 0.04),

showing that the power for 39 Hz ASSR (*M* = 0.12, *SD* = 0.35) was higher than the power for 41 Hz (*M* = 0.23, *SD* = 0.22). No other effect was statistically significant.

The occipital alpha power ([8 14] Hz) averaged over O1 and O2 electrodes, exhibited a significant difference between standing and walking. Specifically, the t-tests showed that the alpha power was higher during standing than during walking ($t(21) = 2.64$, $p = 0.015$). The alpha power during stepping was also significantly higher than during walking ($t(21) = 2.85$, p = 0.01). The difference between standing and stepping did not reach significance ($t(21) = 1.23$, $p = 0.23$) (Figure ***18b***).

To test whether the ASSR power enhancement was associated with the deceased alpha power during walking, a between-participant correlation was performed between the alpha power difference (stand - walk) and ASSR power difference (stand - walk). A significant negative correlation was found ($r = -0.44$, $p = 0.03$, Figure ***18c***), showing that lower alpha power was associated with higher ASSR power.

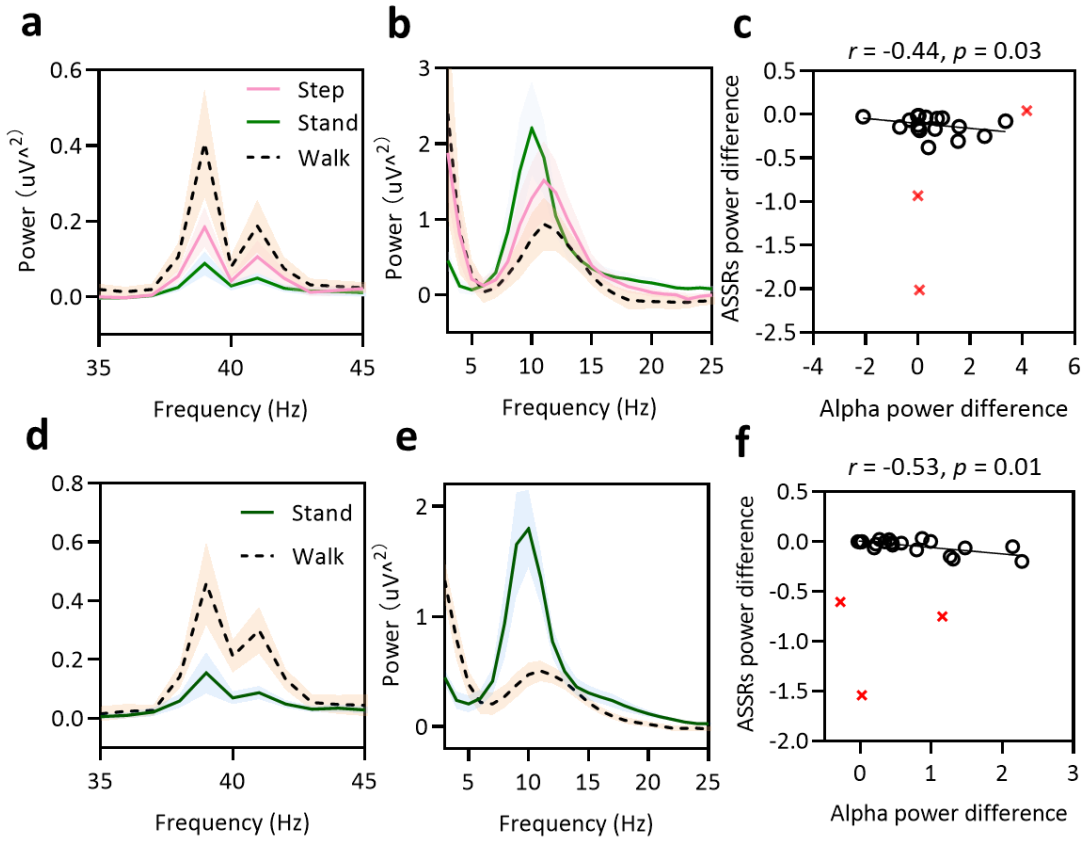

Figure 18. ASSR power and alpha power during different movement conditions. (***a***) The power between 35 and 41 Hz, averaged over frontal electrodes F3 and F4 during stepping (solid pink line), standing (green line), and walking (dash black line) conditions is shown for experiment 1. Both the 39 Hz ASSR power and 41 ASSR power were significantly higher during walking compared to stepping, and were higher compared to standing. Shading lines indicate ± standard error. (***b***) The power averaged over the two occipital electrodes (O1 and O2) is shown between 3 and 25 Hz during stepping, standing and walking for experiment 1. The average alpha power ([8 14] Hz) was significantly higher during standing compared to stepping and was the smallest during walking. (***c***) The ASSR power during (averaged over 39 and 41 Hz) was negatively correlated with the alpha power (stand-walk) averaged over ([8 14] Hz). Three outliers (marked with red crosses) were excluded. (***d***), (***e***) and (***f***) The same is shown for experiment 2, accordingly, only standing and walking condition was present. The results replicated the walking-induced modulation of ASSR power (***d***), alpha power and a significant correlation between alpha power and ASSR power (***f***) as shown in experiment 1.

The enhanced ASSR power and decreased alpha power during walking were replicated in experiment 2. We first tested whether walking leads to an enhanced ASSR power during walking compared to standing. To this end, t-tests were performed separately for the 39 Hz and 41 Hz ASSR power between standing and walking. The results showed that the 39 Hz ASSR power was significantly higher during walking than during standing ($t(27) = -3.30$, $p = 0.002$) and the 41 Hz ASSR power was also significantly higher during walking than during standing ($t(27) = -3.45$, $p = 0.001$) (Figure ***19d***). We then performed t-tests comparing the alpha power between standing and walking. The results showed that alpha power was smaller during walking compared to standing ($t(24) = 4.53$, $p < 0.0001$) (Figure ***19e***). Moreover, the correlation between the modulation of ASSR power and alpha power was also significant ($r = -0.53$, $p = 0.01$) (Figure ***19f***).

5.4.2 The strength of ASSR lateralisation is modulated by the walking path

Experiment 1

The average ASSR modulation index for the left and right turn was computed to index the lateralisation of entrainment. A cluster-based permutation t-test between left turns and

right turns revealed a significant difference between the two turn directions during the time window before the middle turn time point ([-1.20 -0.55]) s (p = 0.02) as well as after the middle turn time point [0.16 0.94]s (p = 0.016) (Figure ***19a***).

As the ASSR modulation index was calculated as the weighted difference using the left side ASSR power (39 Hz) subtracted from the right side ASSR power (41 Hz), a more positive index would indicate a comparatively stronger left side entrainment. When indicating the stronger entrainment direction with an arrow, one can appreciate that the stronger entrainment power is always in line with the turning direction, i.e. for a left turn (red), the stronger entrainment direction always pointed to the left side and for a right turn (blue) the stronger entrainment direction always pointed to the right side. Even if that means that the ASSR LI had to change with respect to the participant's view: the stronger entrainment side before 0 time point is directed inward (aligned with the turn direction and to the left side of the participant); when the participant walked towards the turn direction (i.e. around the 0 time point), the entrainment was more balanced between left and right, suggesting a forward orientation with respect to the participant; after the 0 time point, the entrainment is directed outward (opposite to the turn direction and to the participant's right).

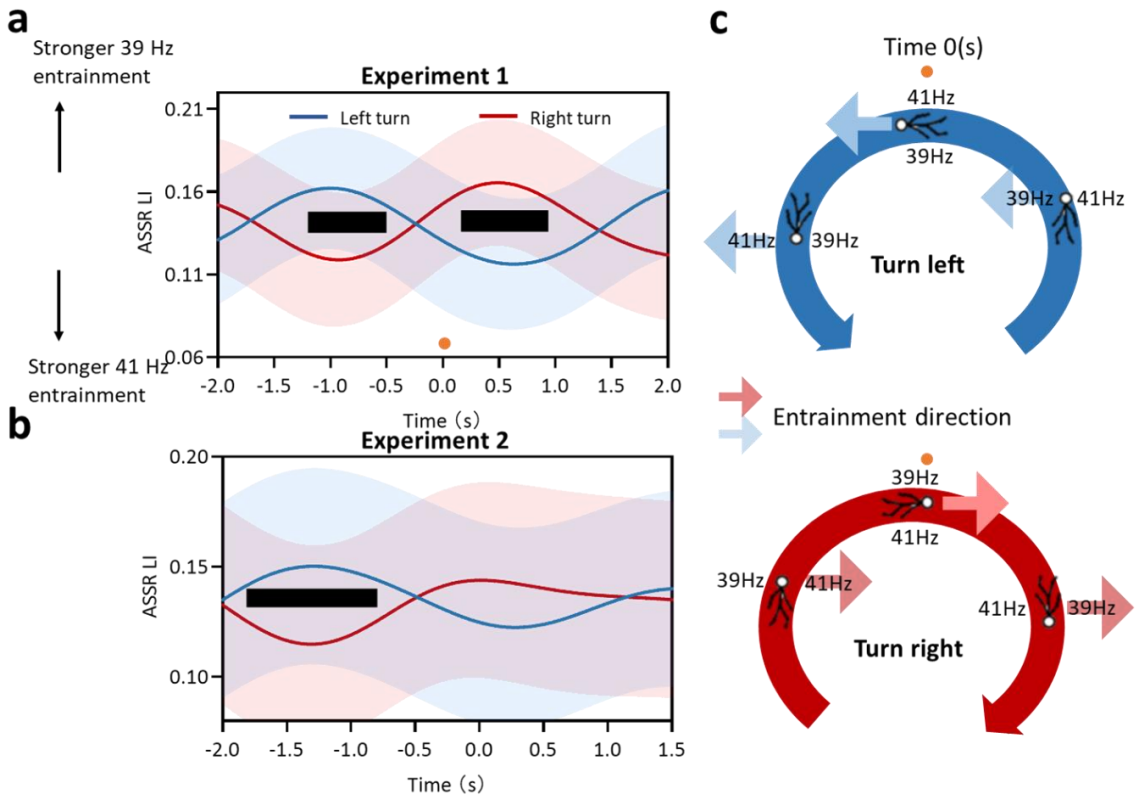

Figure 19. The ASSR lateralisation index is modulated by the walking path. (***a-b***) The ASSR lateralisation index (abbreviated as ASSR LI in the figure) showed a different pattern dependent if the subjects executed a left turn (blue lines) or a right turn (red line). Before time point 0 (marked with an orange dot in the schematic walking path in **c**), the ASSR LI was significantly more positive for the left turn in both experiment 1 and experiment 2. This indicates that the power of the 39 Hz ASSR (presented to the left ear) was stronger than the 41 Hz power (presented to the right ear). In the time window 500 ms before time point 0, the 39 Hz and 41 Hz power was similar. After time point 0, the ASSR LI was significantly more positive for the right turn, indicating that the 41 Hz ASSR power was now stronger than during the left turn. The shaded area indicates ± standard error. The black thick line marks the time windows of significance (FDR adjustment for multiple comparisons). (***c***) The walking direction and the position of the left (39Hz) and right (41Hz) ear entrainment within a turn is indicated by the stick figure and the frequency labels. The arrows indicate the side of stronger entrainment as shown in **a** and **b**.

Experiment 2

Experiment 1 was designed and optimized for the ASSR lateralisation analysis whereas experiment 2 was designed to analyse the processing of a perturbation. Nevertheless, we tested whether the modulation of ASSR lateralisation by the walking path can be observed in experiment 2 despite the presence of perturbation stimuli. Indeed, the ASSR modulation index showed the same pattern (Figure ***19c***) as experiment 1. The cluster-based permutation t-test between left turn and right turn revealed a significant difference between left turn and right turn during the time window before time point 0 ([-1.8 -0.8] s) (p = 0.006). However, the difference between left turn and right turn did not reach significance after the middle time point.

5.4.3 Peripheral ASSR amplitude perturbation modulation was enhanced during walking

To test hypothesis 4, i.e. that peripheral perturbation would more strongly affect the ASSR signal during walking, a three-way (movement state: stand vs. walk; perturbation location: perturbation location: left vs. right vs. central; ASSR frequency; 39 vs. 41) repeated-measures ANOVA was performed. As dependent variable we used the mean perturbation of the ASSR amplitude (39 Hz and 41 Hz, respectively) in the frontal electrodes (F3, F4) during [0 700] ms after the burst tone onset. Results showed a significant interaction between movement state, perturbation location, and ASSR frequency (F(2, 54) = 3.54, p = 0.04). Further, post-hoc t-tests indicated that when the burst tone appeared in the left channel (perturbing the 39 Hz tone), the 39 Hz ASSR amplitude perturbation was more strongly modulated during walking (M= -1.42, SD = 1.36) compared to standing (M = - 1.87, SD = 1.09; t(27) = 2.12, p = 0.04) (Figure ***20a***). Similarly, when the burst tone appeared in the right channel (perturbing the 41 Hz tone), the 41 Hz ASSR amplitude perturbation was more strongly modulated during walking (M = -1.75, SD = 1.27) compared to standing (M= -1.60, SD = 1.00; t(27) = 2.05, p = 0.05) (Figure ***20b***). When both 39 Hz and 41 Hz tones were interrupted by a burst (central tone), no significant difference was observed between standing and walking for neither 39 Hz ASSR perturbation (t(27) = 0.82, p = 0.41) nor 41 Hz ASSR perturbation (t(27) = 0.21, p = 0.84) (Figure ***20c***). Additionally, a significant main effect of ASSR frequency was observed (F(1,27) = 15.26, p < 0.001), indicating that the 39 Hz ASSR amplitude (M = -1.75, SD = 1.27) was more strongly modulated than the 41 Hz ASSR amplitude (M = -1.67, SD = 0.94). No other significant effects were found.

We also investigated whether the difference in ASSR perturbation between standing and walking (average over perturbation locations) could be predicted by the movement dependent difference in ongoing alpha power. However, the correlation analysis yielded a non-significant result (r = -0.18, p = 0.19), indicating that the modulation of ASSR perturbation during free walking was not associated with the modulation of ongoing alpha activity during walking.

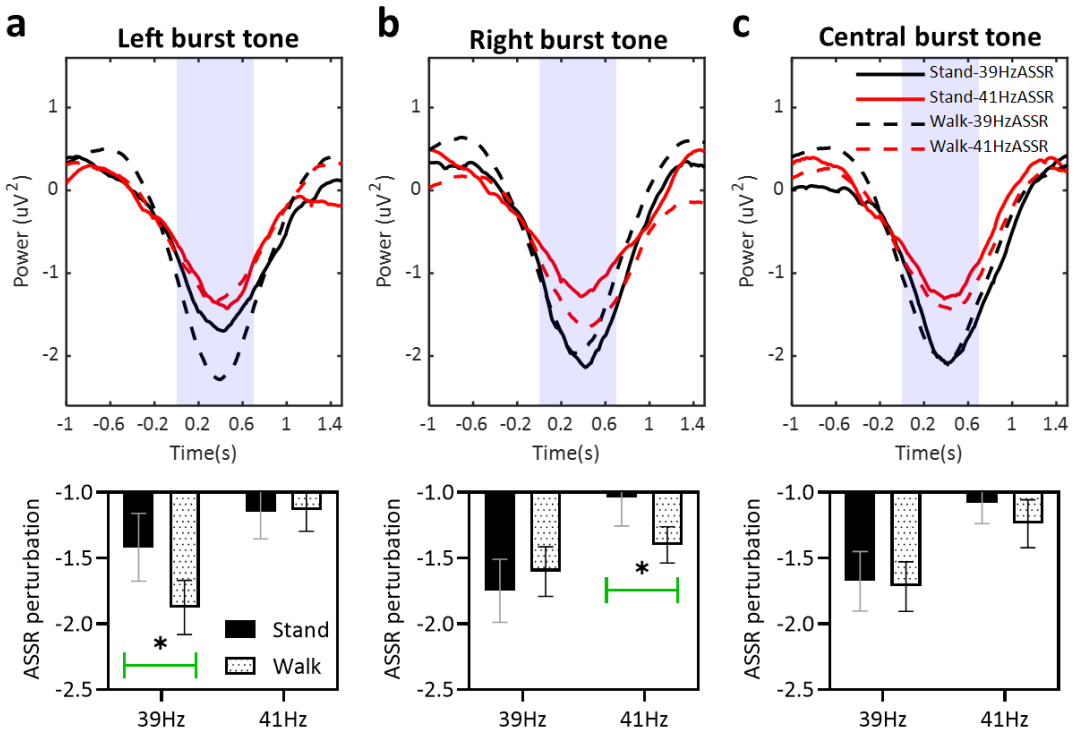

Figure 20. *ASSR amplitude perturbation induced by burst tones during walking compared to standing. (**a**) The ASSR amplitude perturbation (introduced by a left burst tone starting at time point 0 s) is shown for standing (solid line) and walking (dashed line) and for the 39 Hz ASSR (black) and the 41 Hz ASSR (red). (**b, c**) Same as a but for the right burst tone or left and right simultaneous (central) burst tone, respectively. (**d**) The comparison of the ASSR amplitude during ([0 0.7]s, marked with purple) for a left burst tone showed a significantly stronger change due to the burst tone during walking compared to standing for the 39 Hz ASSR amplitude perturbation (left side ASSR) but not for the 41 Hz ASSR amplitude perturbation (right side ASSR). (**e**) When the burst tone appeared on the right side, only the 41 Hz ASSR amplitude perturbation was more strongly affected by the tone during walking compared to*

*standing (**f**). When both 39 Hz and 41 Hz tones were interrupted by a burst tone, no significant difference was observed between standing and walking. Asterisks* indicate p < 0.05.*

5.4.4 Modulation of peripheral ASSR perturbation was not dependent on the walking path

In a next step, we investigated whether the strength of the peripheral ASSR perturbation was dependent on the walking path by testing if the strength was different between turn directions. First, the perturbation trials were grouped based on the perturbation side (left side – 39 Hz, right side – 41 Hz) and whether the perturbation happened during a left or a right turn (Figure ***21a***, left turn path is marked in blue, right turn path is marked in red). A 3-way (turn direction: left vs. right; perturbation location: left vs. right vs. central; ASSR frequency: 39 Hz vs. 41 Hz) repeated-measures ANOVA was performed with the average ASSR amplitude perturbation between the two lateralised frontal electrodes amplitude (F3, F4) during [0 0.7]s after the burst tone onset. In addition to the main effect of ASSR frequency ($F(1, 27) = 11.58$, $p = 0.002$); only the interaction between the perturbation location and the ASSR frequency was significant ($F(2, 54) = 5.58$, $p = 0.008$): the 39 Hz ASSR amplitude was most strongly modulated in the left perturbation condition while the 41 Hz ASSR amplitude was most strongly modulated in right perturbation condition. No other effect was found to be statistically significant, including the interaction between turn direction, ASSR perturbation, and ASSR frequency ($F(2, 54) = 1.82$, $p = 0.17$).

However, as we saw that the ASSR was modulated by the turn direction in such a way that the lateralisation flipped around time point 0, thereby always preferring the absolute direction of the run, we also tested the perturbation strength accordingly. The perturbation trials were therefore grouped based on whether they happened in the time during which the left ear input (39 Hz) or the right ear input (41 Hz) was preferred (Figure ***21c***, stronger left entrainment time was marked in blue, stronger right entrainment was marked in red). However, the 3-way (stronger entrainment direction: left vs. right; perturbation location; left vs. right vs. central; ASSR frequency: 39 Hz vs. 41 Hz) repeated-measures ANOVA with the perturbation power between ([0 0.7]s) only showed a significant main effect of ASSR frequency ($F(1, 27) = 7.17$, $p = 0.01$). This suggests that the 39Hz ASSR perturbation amplitude was more strongly modulated compared to 41 Hz ASSR amplitude. No other effects were statistically significant.

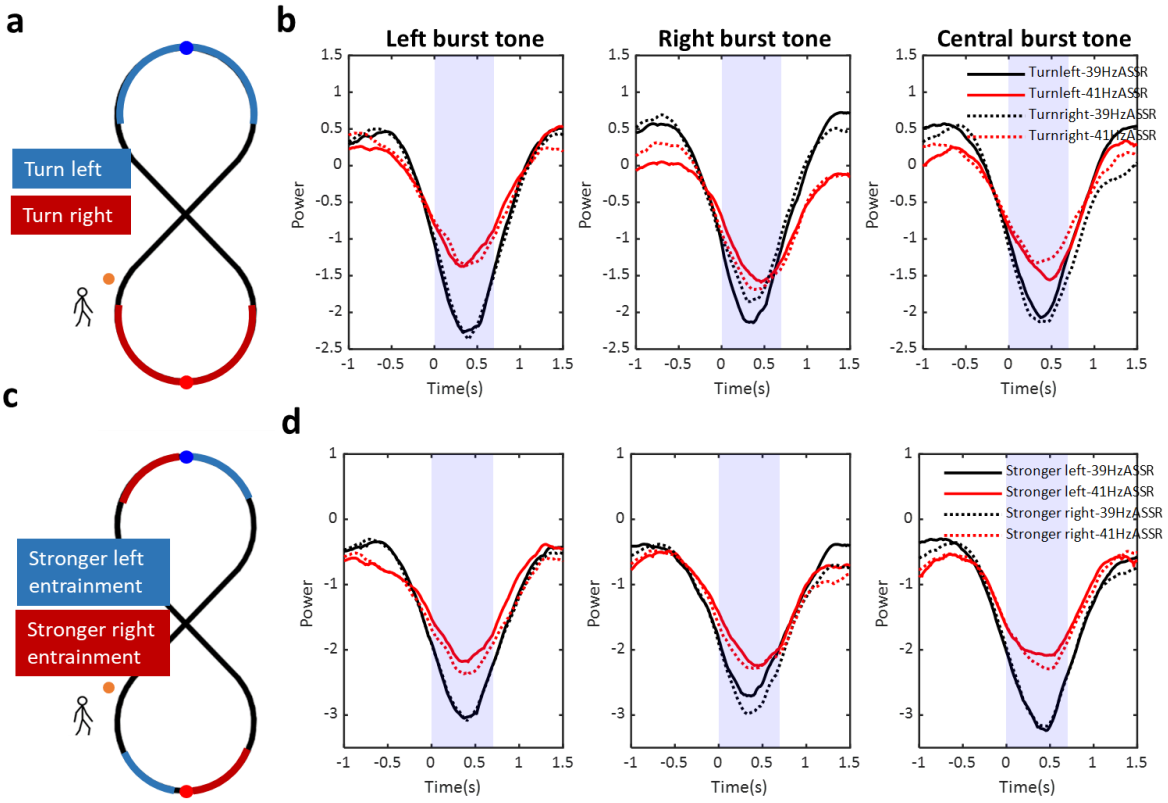

Figure 21. *The modulation of peripheral ASSR perturbation during walking.* ***(a)*** *The perturbation grouping (solid and broken lines) as shown in (b) was based on a [+\- 2 s] time window around the time point of local maximum/minimum (marked with a dot) during the left turn (blue) and right turn (red).* ***(b)*** *The 39 Hz amplitude perturbation (plotted in black) and 41 Hz amplitude perturbation (plotted in red) are shown separately if happened during the left turn (solid lines) and right turn (dashed lines), for the left burst tone (left panel), right burst tone (central panel), and central burst tone (right panel) conditions. The amplitude perturbation was statistically compared average over the time window between ([0 0.7]s) was specifically compared (marked in purple).* ***(c)*** *The perturbation grouping (solid and broken lines) as shown in (d) was based on a [2 s] time window before (blue) and after (red) the time point of local maximum/ minimum (marked with a dot) during the left and right turn.* ***(d)*** *Same as b but grouping was based on the time periods marked in (c).*

5.4.5 ERP locked to the burst tone onset

We conducted an additional ERP analysis of the data from experiment 2. The ERP locked to burst onset (average over two frontal electrodes F3 and F4) was analysed, specifically focusing on the P1 component ([150 190]ms) and the P2 component ([300 350] ms). First, a repeated-measures ANOVA with a two-way design (movement state: stand vs. walk; perturbation location: left vs. right vs. central) was performed, revealing a significant main effect of movement state ($F(1, 27) = 11.70$, $p = 0.001$). The P1 amplitude was higher during walking ($M = 0.18$, $SD = 0.74$) compared to the standing condition ($M = -0.38$, $SD = 0.82$) (Figure ***22a-c***, marked in green). No other effect reached statistical significance.

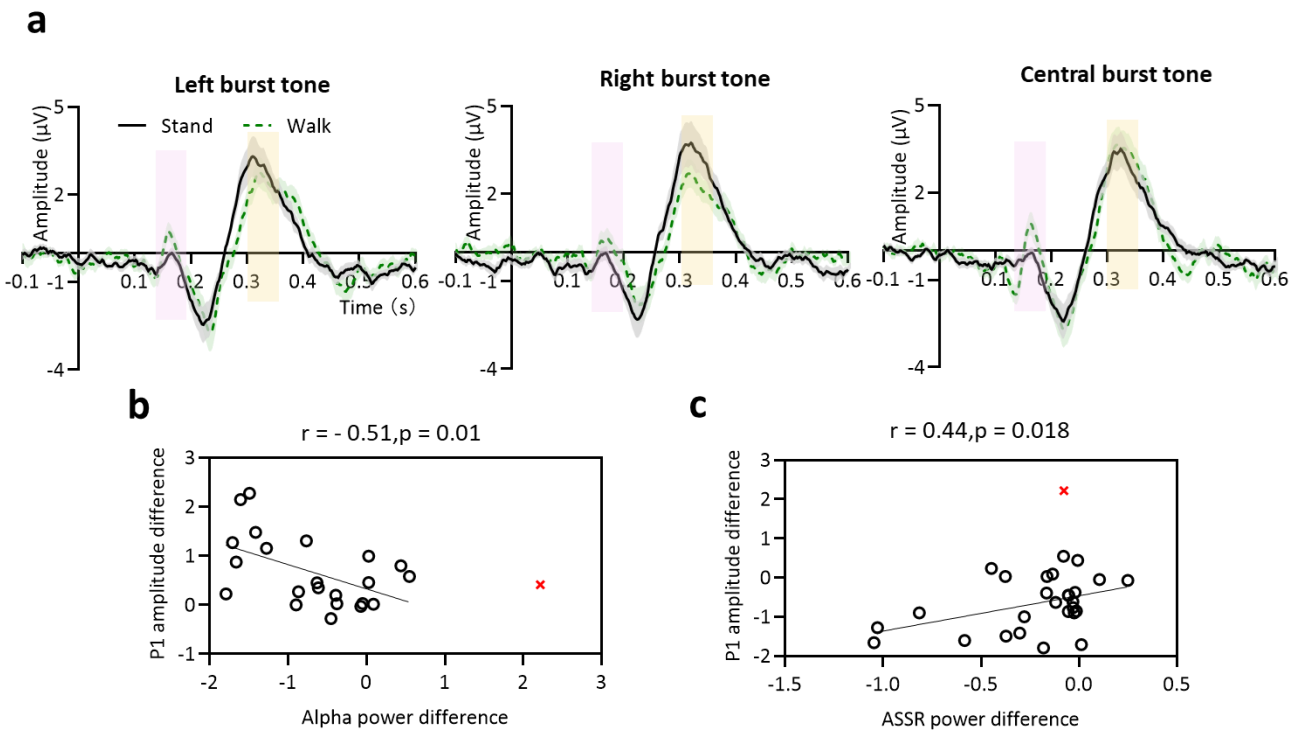

Figure 22. *The ERP time-locked to the burst tone onset. (**a**), The ERP waveform averaged over the F3 and F4 electrode I shown time-locked to a left burst tone, a right burst tone, and central burst tone during standing (solid line) and walking (dashed line). The shaded pink and yellow box represents the time window of P1 ([150 190] ms) and P2 ([300 350] ms) component. (**d**) The modulation of the P1 amplitude (stand - walk) negatively correlated with the modulation of ongoing alpha power (stand - walk). (**e**) The modulation of the P1 amplitude (stand - walk) positively correlated with the modulation of the ASSR power (average between 39 and 41 Hz) (stand - walk).*

We further investigated the relationship between the P1 amplitude with ongoing alpha oscillations and ASSR power. The modulation of the P1 component amplitude was negatively correlated with the modulation of ongoing alpha power (stand - walk) (r = -0.51, p = 0.01) (Figure ***22d***). This indicated that lower ongoing alpha power was associated with a higher P1 component. Furthermore, the modulation of the P1 component amplitude was positively correlated with the modulation of ongoing alpha power (stand - walk) and ASSR power (r = 0.44, p = 0.018) (Figure ***22e***).

We also analysed the P2 component ([300 350] ms) using the same two-way repeated-measures ANOVA. We found a significant main effect of perturbation location (F(2, 54) = 5.52, p = 0.01), indicating that the central perturbation condition (M = 3.24, SD = 2.72) resulted in a stronger P2 component compared to the left perturbation condition (M = 2.63, SD = 2.56), and was also higher than the right perturbation condition (M = 2.90, SD = 2.77). Additionally, we observed a significant interaction between movement state and perturbation location (F(2, 54) = 5.43, p = 0.01), which indicates that the P2 component amplitude was smaller during walking in the two peripheral conditions (average between left and right perturbation: t(27) = 2.31, p = 0.03) but showed no significant difference in the central locations (t(27) = -1.00, p = 0.32) (Figure ***22a-c***, marked in yellow). Interestingly, further exploratory correlation analysis showed that the modulation of the P2 amplitude neither correlated with the ASSR perturbation modulation (r = 0.17, p = 0.39) nor correlated with the ongoing alpha oscillation modulation (r = - 0.29, p = 0.14).

5.5 Discussion

Investigating the influence of natural walking on brain activity, we replicated the previously reported reduction in occipital alpha power during walking compared to standing in both our experiments. Through the analysis of ASSR, ASSR perturbation and ERPs, we could show that walking enhanced auditory processing, partly in a spatially specific way. The decreased alpha power due to walking was linked to the increased auditory entrainment. Further, the lateralisation of auditory entrainment was modulated by the walking path. Below we will discuss the putative underlying mechanism of the enhanced (peripheral) sensory processing during walking and the possible role of these walking induced neural modulations in active sensing. Additionally, we showed that the strength of the auditory entrainment was

significantly stronger during forward walking compared to stepping-in-place and standing. This suggests natural walking to be the relevant feature, which will also be discussed below.

5.5.1 Enhanced sensory processing during walking

In the current study, we found that walking led to an enhanced ASSR power compared to standing. The ASSR is an electrophysiological measure of brain activity that reflects the entrainment of neural activity to a rhythmic auditory stimulus (Galambos et al., 1981; Picton et al., 2002; Picton et al., 2009). Many previous studies have identified the cortical sources of the ASSR within the primary auditory cortex (A1) using magnetoencephalography (MEG) (Herdman et al., 2003; Ross, Herdman, & Pantev, 2005a; Teale et al., 2008). ASSR has further been utilized as an indicator of sensory processing dysfunction in clinical settings as well as reduced hearing ability in hearing tests (Picton, Dimitrijevic, Perez-Abalo, & Van Roon, 2005; Sugiyama et al., 2021). The enhanced ASSR power during walking therefore suggests enhanced sensory processing in the early auditory cortex. This auditory enhancement during walking corresponds well to the findings in the visual domain, for which a higher occipital SSVEP power (induced by ongoing rhythmic visual stimulation) was observed during stationary cycling compared to sitting (Bullock, Elliott, Serences, & Giesbrecht, 2017).

In addition to the ASSR power enhancement while walking compared to standing, we also observed amplification in the amplitude of the first positive ERP component (P1) following a burst tone. This component was observed approximately 150 ms after the burst tone onset. However, as the P1 component usually appears around 50 ms after stimulus onset (Hillyard & Anllo-Vento, 1998), we assume that it was actually introduced by the burst tone offset (the burst tone lasted for 100 ms), which is equivalent to the ASSR tone onset after the burst. Previous studies already have reported an increase in sensory evoked potentials due to natural movement. Particularly, the early negative ERP, namely N1, was increased in amplitude due to walking in the auditory domain Scanlon et al. (2019) as well as the visual domain (Chen et al., 2022a, 2022b). Overall, the modulation of early auditory ERP components together with the increased ASSR signal provides support for the notion of enhanced processing of auditory input due to natural walking.

5.5.2 Enhanced peripheral processing

Work in the visual domain has suggested that the sensory processing particularly in the periphery is affected by body movement. Enhanced peripheral sensory processing during walking compared to a stationary state has been previously reported in animal (Ayaz et al., 2013) and human visual research (Benjamin et al., 2018; Cao & Händel, 2019; Reiser et al., 2022). In the experiments at hand, two different auditory ASSR tones were presented, one in the left ear and the other in the right ear. The setup therefore created peripheral auditory input. Unfortunately, as we had no central ASSR stimulus, we are unable to directly test whether the walking induced increase in ASSR was confined to peripheral input or rather a general effect. To investigate this in future work, the perceptual experience as to peripheral or central input should be checked and a condition should be included where two ASSR tones with the same frequency are presented to both ears, thereby creating a central auditory input. Such a condition however, could be analysed in experiment 2 as we presented a burst tone to either the left ear, the right ear or both ears at the same time. The burst tone presented to the left or right ear is perceived as peripheral input whereas the burst tone presented to both ears is perceived as coming from a central location. The results of the analysis of burst tone-induced ASSR amplitude perturbation shows that only burst tones that appeared in the periphery reduced the ASSR amplitude of the corresponding frequency (i.e. a left burst tone reduced the left 39Hz ASSR signal, a right burst tone reduced the right 41Hz ASSR signal). This is a very interesting finding as it not only suggests enhanced peripheral processing of auditory input during walking, but also excludes that the increased perturbation response was simply a side effect of increased ASSR power during walking. If this had been the case, also a walking induced effect of the central perturbation would have been expected.

The ERP analysis further revealed that the second positive ERP component (P2) following a burst tone was smaller during walking compared to standing for the peripheral burst tone condition only. P2 appeared around 200 ms after the ASSR tone onset (burst tone offset). The reduction of the P2 amplitude stands in contrast to the increased amplitude in ASSR perturbation. This suggests, that they are caused by different underlying neural processes. For the ASSR amplitude perturbation, the reduction in entrainment was suggested to be due to a change in ongoing auditory input (Ross, Herdman, & Pantev, 2005b), whereas the auditory ERP is believed to reflect the processing of a new sensory event (Teder-Salejarvi, Hillyard, Roder, & Neville, 1999). Accordingly, it makes sense that we did not find a

relationship between modulations of ASSR amplitude perturbation and the P2 component. What does the pattern of the P2 component reflect? The functional significance of the P2 component is still not fully understood. It is thought to index some aspects of stimulus classification, reflecting primary processes of attentional allocation, perceptual learning, and even memory (for a review, see Crowley & Colrain, 2004). However, one crucial view of the P2 component is that it is associated with inhibitory processes and protection against interference from irrelevant stimuli (Garcıa-Larrea et al. 1992; Senderecka et al. 2012), with stronger inhibition leading to a stronger P2 amplitude. Previous research has reported a frontal enhancement in P2 amplitude for participants who underwent inhibition training compared to those who underwent discrimination training (Melara, Rao, & Tong, 2002). In the inhibition training, subjects were systematically exposed to progressively stronger intensities in irrelevant signals to improve their ability to suppress distracting events while participants undergoing discrimination training were given prolonged practice in a one-channel oddball procedure in the absence of distraction. Considering the above-mentioned findings associating an increased P2 with increased inhibition, the current finding of a reduced P2 component during walking compared to standing might suggest that walking leads to reduced inhibition of the peripheral auditory input. This would indeed be in line with the reported enhanced peripheral processing during walking and its link to inhibition, as will be discussed below.

During natural walking, individuals are exposed to a dynamic and changing environment, with stimuli appearing from various spatial locations. This increased spatial complexity might require heightened sensory processing to detect and analyse relevant information. The significance of particularly peripheral vision during locomotion has been previously acknowledged (Vater & Strasburger, 2021; Vater, Wolfe, & Rosenholtz, 2022). Indeed, the peripheral visual input is crucial for interpreting the visual flow field to know the speed and direction of movement (Banton, Stefanucci, Durgin, Fass, & Proffitt, 2005; Turano, Yu, Hao, & Hicks, 2005). My findings in the auditory domain suggest that the importance of increased peripheral processing extends beyond vision. It might be an across-modality enhancement that contributes to the perception of object movement in the surrounding environment (Rogers, Rushton, & Warren, 2017) and ultimately assists navigation.

5.5.3 Enhanced sensory processing related to alpha power and the possible underlying mechanism

In both experiments, we replicated the robust finding of a decreased alpha power due to body movements in humans (Cao et al., 2020; Ehinger et al., 2014; Kuziek et al., 2018; Lin et al., 2014; Nenna et al., 2020; Robles et al., 2021; Scanlon et al., 2019; Shaw et al., 2018; Vaughn et al., 2021; Wagner et al., 2019; Zink et al., 2016). Importantly, we also found that the decreased alpha power due to walking was significantly correlated with the modulation of ASSR power and auditory evoked P1 component amplitude due to walking. These results are in line with previous findings in the visual and auditory domain. A concurrent change in alpha power and ERP or entrained signals has been reported repeatedly, however, a direct correlation has not always been tested (Bullock et al., 2017; Ehinger et al., 2014; Kuziek et al., 2018; Peskar et al., 2023; Robles et al., 2021; Scanlon et al., 2019; Vaughn et al., 2021). E.g. Scanlon et al. (2019) reported an enhanced amplitude of the auditory N1 component and a reduced parieto-occipital ongoing alpha power during cycling compared to stationarity. Similarly, Vaughn et al. (2021) found that the auditory Mismatch Negativity (MMN) component amplitude was greater during riding compared to sitting, while the occipital alpha power was smaller. However, they both did not analyse the relationship between alpha power and ERP components. Only recently, a study has confirmed a correlation between the visual N1 component and occipital alpha power modulation due to body movement, (Chen et al., 2022b). Additionally, work by Cao and Händel (2019) showed that sorting trials based on their SSVEP power led to a significant difference in alpha power, demonstrating also a connection between alpha power and entrained signals.

We had already previously proposed that, as occipital alpha power likely marks an inhibitory process (Händel, Haarmeier, & Jensen, 2011; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007b), inhibition may serve as a mechanism through which walking influences early sensory processing in visual tasks (Chen et al., 2022b). The idea that the modulation of ongoing alpha oscillation due to body movement is introducing a change in sensory processing is indeed further supported by our findings.

Interestingly, those effects that were exclusively found for the peripheral auditory processing (ASSR perturbation and P2), were not correlated with the occipital alpha power

effects due to walking. Indeed, this is in line with a finding from the visual domain where only the early ERP was correlated with alpha power but not affected by eccentricity, whereas the later ERP was modulated by peripheral input, specifically, but not related to the ongoing occipital alpha power modulation due to walking (Chen et al., 2022b). The current study provides evidence from the auditory domain that sensory processing marked by the temporally early evoked potential are different from sensory processing marked by later evoked potentials as they are differentially affected by walking.

Overall, our findings are congruent with the idea the walking modulates occipital alpha power, which marks reduced inhibition, hence leading to increased sensory processing. Through a second independent process, walking also influences the processing of peripheral sensory input. We want to shortly mention that these modulations might be corresponding to an attentional process.

5.5.4 The strength of sensory entrainment is modulated by the walking direction

During walking, we found that the processing of ongoing peripheral auditory input was modulated with respect to the walking path. We calculated an ASSR lateralisation index by comparing the responses to the different frequencies presented to the left and right ear. By comparing the ASSR modulation index between left turns and right turns, a distinct ASSR modulation index pattern was observed during different time periods while turning. The pattern showed that the stronger entrainment power was always in line with the turning direction, i.e. for a left turn, the stronger entrainment direction always pointed to the left side; for a right turn, the stronger entrainment direction always pointed to the right side (see Figure ***19a***). This means that the ASSR lateralisation index had to change with respect to the participant's view: the stronger entrainment side before reaching the vertex is directed inward (aligned with the turn direction and to the left side of the participant); when the participant walked towards the turn direction (i.e. around the vertex), the entrainment was balanced between left and right, suggesting a forward orientation with respect to the participant; after the vertex, the entrainment is directed outward (opposite to the turn direction and to the participant's right).

The active sensing framework proposes that the motor system can influence perception by directly generating sensory input through the execution of motor actions (for reviews, see (Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010; Yang, Wolpert, & Lengyel, 2018). This could result in a systematic pattern of eye movements and fixations to gather visual input, in a modulation of head orientations to adapt the auditory input and sniffs to generates airflow and affect odor perception. During human walking, Turano, Geruschat, and Baker (2003) provided evidence that while participants walk to a target, their eyes tend to move in a way that takes into account both the overall features of their surroundings and the specific geographic information related to the target. Also Sprague and Ballard (2003) demonstrated that the gaze is adapted to the walking path while interacting with various elements, such as sidewalks, obstacles, and litter. An active change in eye movements is also reported for other natural behaviours such as sports, and making tea or sandwiches (for reviews, see (Mary Hayhoe, 2000; M. Hayhoe & Ballard, 2005) In such a way, active sensing shapes the specific content of sensory information flowing from the bottom up (Morillon, Hackett, Kajikawa, & Schroeder, 2015).

However, in the current experiments, the auditory input was played via a pair of inserted earphones, and the volume was adjusted to a level where it surpassed the threshold for perceiving other external auditory input. Such an experimental set-up ensured that the auditory input remained unchanged regardless of the participants' head orientation or body movements. This means, that a path related adaptive change in motor output did not affect the auditory input and therefore cannot have caused the neural response modulation. We therefore propose that here a mechanism is at play that operates in a top-down fashion to modulate sensory processing during walking. A review of top-down control in the active sensing framework, particularly with respect to rhythmic sampling, can be found in the work by Morillon et al. (2015).

What might be the specific top-down control in our experiments? Previous studies which examined changes in ASSR signals in response to left- and right-sided stimuli have demonstrated a change in ASSR amplitude due to spatial attention. Specifically, more attention to a particular side led to an enhanced ASSR amplitude in the corresponding side (Bharadwaj, Lee, & Shinn-Cunningham, 2014; Manting, Andersen, Gulyas, Ullen, & Lundqvist,

2020; Ross, Picton, Herdman, & Pantev, 2004; Skosnik, Krishnan, & O'Donnell, 2007; Voicikas, Niciute, Ruksenas, & Griskova-Bulanova, 2016). Accordingly, the modulation of ASSR lateralisation observed in our studies might reflect a shift of attention dependent on the walking path. This interpretation suggests that active sensing goes beyond an active orchestrating of the sensors and additionally includes a shift in attentional processes. Such behaviour might serve to optimize navigation during natural walking.

It is interesting to speculate why this pattern was so stable across subjects that we could find it via group analysis. One idea is that, as the walking path was pre-defined and simple to remember, participants might have mentally encoded the path in a map-like fashion. By encoding the spatial layout of the pathway in their minds, they first have a global direction, e.g. a generally left turn or right turn. As the same time, during walking, participants could effectively anticipate upcoming turns and adjust their attention accordingly in an active sensing manner. This adjustment might be reflected in the changing inward-forward-outward attentional patterns observed in the analysis of the ASSR lateralisation from the participants' view.

5.5.5 Natural walking is most effective

When comparing the two movement conditions in experiment 2, we found a stronger enhancement of ASSR power during walking compared to stepping. These two conditions are similar in motor output and auditory and somatosensory feedback, but only walking leads to a change in spatial position while stepping is stationary. Accordingly, as we found a significant difference in ASSR power between the two conditions, we show that the walking-induced effect on auditory entrainment was not based on non-visual sensory feedback e.g. walking movement causing somatosensory input, or the footfall causing auditory input. Similarly, it is not the engagement in stepping movements per se that leads to a neural change. Could the difference be caused by the aspect of locomotion during walking? This is unlikely as previous work has shown that locomotion that is not based on motor output is not effective. A study by Vaughn et al. (2021) examined the neural marker of sensory processing known as the MMN component during cycling and driving (Vaughn et al., 2021). They found that the MMN amplitude was larger during cycling compared to driving. This implies that merely moving forward without bodily engagement is insufficient to enhance sensory processing.

We therefore propose that it is natural movement that introduces the strongest changes in sensory processing. We would define natural movement as motor output that has a certain ecologically valid aim such as going from one place to another. Indeed, all studies that provided evidence for a general enhancement of early sensory processing due to body movements, tested natural body movements such as natural walking (Chen et al., 2022a, 2022b), and outdoor cycling (Malcolm, Foxe, Butler, Molholm, and De Sanctis (2018) and Vaughn et al. (2021). This could also partially explain why some studies did not observe a statistically significant effect on sensory processing when participants were asked to do non-natural walking like walking on a treadmill (Gramann, Onton, et al., 2010; Malcolm, Foxe, Butler, & De Sanctis, 2015; Nenna et al., 2020).

5.5.6 Further considerations and possible limitations of the current study

Several factors are important to consider and call for further experiments. Firstly, it is important to address the issue of eye movements. Since eye movement data were not recorded, it remains unknown whether the modulation of sensory processing by the walking path is linked to a walking path related eye movement pattern. As reviewed above, eye movements are known to change with respect to the visual demands of a path (Mary Hayhoe, 2000; M. Hayhoe & Ballard, 2005; Sprague & Ballard, 2003; Turano et al., 2003) and a recent study showed that saccades can modulate the neural excitability of the auditory system (Leszczynski et al., 2023). It therefore will be relevant to understand if the change in auditory processing coincides with changed eye movements. However, it is important to keep in mind that even if this is the case, it will not be clear if a conjoint modulation of e.g. attention is the underlying mechanism as the eye movement itself does not influence the auditory input.

Secondly, it will be interesting to explore whether the standardized neural pattern was primarily due to the predictability of the walking path. By introducing unpredictability into the path, one could evaluate whether the observed standardized pattern persists or if it varies under different conditions. Nevertheless, we want to highlight that the fact, that there was a modulation in auditory processing due to walking and the walking path, despite unchanged auditory input, excludes the possibility that the sensory processing enhancement is based on visual prediction. While walking related changes reported in the visual domain could have been based on the preparation of the system to predictable visual input, this is not possible

for the auditory domain in a low-level fashion. In fact, a previous study has shown that early sensory processing marked by steady-state responses was exclusively modality-specific (Porcu, Keitel, & Muller, 2014). Although there could still be a potential visual-auditory interaction, such interaction would not be based on a low-level effect. Our findings based on the entrained auditory response therefore strongly suggest a more general and higher-level effect of natural walking on sensory processing.

Thirdly, a behavioural task can help understand in how far the change in the neural signals marking sensory processing coincides with perceptual changes. Indeed, work in the visual domain suggest that the relationship is complex and that the effect of walking differs across processing stages (Bullock et al., 2015; Chen et al., 2022a, 2022b). These studies have indicated that perceptual outcomes may be more influenced by the modulation of temporally later processes. Testing for walking related behavioural changes will help understanding if the observed modulation in sensory processing due to the walking path reflects a mechanism to optimize navigation. A pertinent approach would be the use of specific behavioural testing in a navigation task.

5.6 Conclusion

In summary, our studies, based on auditory entrained brain responses, showed that walking led to enhanced auditory processing compared to a stationary state. This enhancement was associated with a walking induced decrease in occipital alpha power suggestive of an underlying mechanism of reduced inhibition while walking. Through the analysis of ASSR perturbation and ERPs, we could further show that walking additionally enhanced auditory processing in a spatially specific way. We suggest that this is part of a strategy to optimize perception during navigation. The most seminal finding however is that the lateralisation of auditory entrainment was modulated by the walking path. It suggests a possible role of these walking induced neural modulations in active sensing which would mean that active sensing goes beyond an active orchestration of the sensors but additionally includes a modulation of how sensory input is processed. Finally, we showed that the strength of the auditory entrainment was significantly stronger during natural walking compared to stepping-in-place and standing, suggesting natural walking to be the relevant feature for the modulation of sensory processing during movement.

5. Study 4

6. Study 5: Reduced occipital alpha power marks a movement induced state change that facilitates creative thinking

Reduced occipital alpha power marks a movement induced state change that facilitates creative thinking

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Abstract

Walking and minimized movement restriction has a positive effect on creativity, such as divergent thinking. Walking is further known to reduce occipital alpha activity. We used mobile EEG during free and restricted movement, while subjects (N=23) solved a Guilford's alternate uses test, to understand if occipital alpha power is also affected by movement restriction and if it is a neural marker for creativity. We found that, independent of the task, relative occipital alpha power was higher during movement restriction and showed a negative relationship with creativity scores even though the task was purely based on auditory information. Alpha lateralisation was only modulated during the task related think-time (mainly during sitting) and showed a positive relationship with creativity scores but no correlation with the relative alpha power. This indicates that the ongoing alpha power and alpha lateralisation mark two independent processes. Overall, our work shows that

movement and movement restriction leads to a general change in state which affects cognitive processes. Specifically, limiting one's movements e.g. due to sitting and fixating on a screen can introduce a state of increased occipital alpha power and lowered creativity.

Keywords: divergent thinking, occipital alpha power, alpha lateralisation, free movement, mobile EEG

6.1 Introduction

Creativity is discussed to be a cognitive feature in which humans might keep excelling artificial intelligence (AI). Accordingly, parallel to the improvement of AI in solving increasingly complex questions, creative thinking will likely become more and more important. At the same time, children seem to grow up in a world in which creativity is of little importance; this is true throughout school education but also for leisure time activities. Children and adolescents spend a high number of hours passively immersed in media. For the year 2021 this was on average 7.7 h/d in the US (Nagata et al., 2022) or 5.2 h/d in Germany (KIM, 2020). Additionally, also formerly creative toys have changed. For example, building blocks such as LEGO are not anymore primarily intended to be used to create new things, but to follow a plan to reach one predefined outcome. Similarly, it is not so much one doll that is flexibly changed to fit different contexts, but pre-styled dolls are used for different play situations.

Given the importance of creativity to solve problems in a fast-changing world, we should strive to understand what fosters creative thinking and what is the neural mechanism behind it. We say this fully aware of the committed simplification as creative thinking is based on various highly complex processes. Nevertheless, specific aspects can be defined. We will focus on divergent thinking, a main process involved in creativity (Guilford, 1967).

A robust finding of recent years is that body movement such as walking can facilitate creative thinking, corroborating a long standing traditional believe. Empirically it has been shown that walking has a positive effect on creativity measures, such as divergent thinking (Oppezzo & Schwartz, 2014). Particularly free walking, in which the path is not predefined but can be chosen freely, improves scores in divergent thinking (Kuo & Yeh, 2016; Zhou et al., 2017). Even more relevant for many modern everyday settings involving a screen is that it is the restriction of ones' movements that has the main effect on creative thinking: e.g. fixating on a screen will reduce divergent thinking scores significantly compared to sitting without any further movement restriction (Murali & Händel, 2022).

One main neural change due to walking is reduce alpha power, i.e. brain oscillatory activity around 10 Hz, over occipital cortex (Ehinger et al., 2014; Lin et al., 2014; Scanlon et al., 2019). A walking induced change in alpha power can even be found in complete darkness

(Cao et al., 2020) which shows that it is not a visual input driven effect. Alpha activity can be viewed as neural marker of attention as attentional modulation towards sensory input leads to a concerted in- and decrease of alpha power over the cortex (Foxe et al., 1998; Thut et al., 2006). The observed decrease for input that is attended and the increase in sites that process information that should be ignored led to the interpretation that alpha activity marks an attention-driven inhibitory process (Händel et al., 2011; Kelly et al., 2006; Klimesch et al., 2007; Rihs et al., 2007). In recent studies, it was established that walking likely broadens the focus of visual attention and that alpha power is related to this broadening (Cao & Händel, 2019).

Interesting work has indicated an importance of attention as well as alpha activity for specific aspects of creativity. The size of the focus of attention has been shown to affect divergent thinking. Test scores were significantly lower if attention was focused on a small central area of the visual field compared to a larger one extending into the periphery (Friedman et al., 2003). More indirect evidence of the involvement of attention comes from studies on inhibition. Using a combination of the classical Guilford's alternate uses test or AUT (Guilford, 1967) for divergent thinking and a Flanker tasks, it has been shown that conditions in which a wrong response had to be more often inhibited led to higher AUT scores (Radel et al., 2015). Inhibition and attention are closely related, and also during a convergent thinking task, alpha power has been reported to decreases over occipito-parietal areas when attention was externally oriented (low inhibition) compared to internally (Benedek et al., 2011).

Interestingly, there is ample evidence that EEG alpha power is also related to processes relevant for creative ideation (Camarda et al., 2018; Fink & Benedek, 2014; Mastria et al., 2021; Razoumnikova, 2000; Stevens Jr & Zabelina, 2020). In general, one can distinguish two main sets of findings: a change in alpha power after task onset with respect to a baseline, and a modulation of alpha lateralisation. Mostly tested with AUT, alpha power changes with respect to a baseline are found in frontal sensors, and over a broad temporo-parieto-occipital area (Fink et al., 2009; Fink et al., 2011). The task is reported to induce an alpha power increase over frontal sensors and a decrease over occipital and parietal sensors (Jauk et al., 2012; Rominger et al., 2019; Schwab et al., 2014). However, others found such alpha modulation only for a convergent task but not AUT (Benedek et al., 2014). More creative

individuals further show a more strongly reduced alpha power (compared to baseline) over occipito-temporal electrodes compared to less creative individuals (Jauk et al., 2012) but were also reported to have an alpha increase in right side fronto-parieto-central electrodes (Grabner et al., 2007) compared to less creative subjects. Indeed, particularly in the right hemisphere, there is a modulation of alpha power over time in frontal and occipital sites during creativity tasks (Rominger et al., 2019). This modulation over time (Rominger et al., 2019) and the difference between left and right alpha power (Schwab et al., 2014) seems related to originality.

To summarize, we know that free walking improves divergent thinking and reduces occipital alpha power, and that alpha activity is somehow related to creative ideation. However, it is not so much the movement but a missing movement restriction that positively affects divergent thinking. In order to further understand if a change in occipital alpha power is introduced by non-restriction and if this occipital alpha power effect is connected to creativity, we tested the following hypotheses:

- Occipital alpha power is reduced during free vs restricted movement state similar to walking vs standing.
- There is a negative correlation between alpha power and creativity.
- Movement restriction introduces a state change independent of the task.
- Alpha lateralisation is linked to the overall alpha power as modulated by the movement condition.

We used mobile EEG during free and restricted movement while solving a Guilford's alternate uses test or AUT (Guilford, 1967) for divergent thinking. Additionally, by presenting all instructions auditorily thereby excluding effects based on the visual processing of the task related input, we tested if the alpha power modulation during AUT is independent of the modality of presentation.

6.2 Materials and Methods

The experiment was part of a previous cohort of studies with which we investigated the role of eye movements and the effect of motor restriction on divergent thinking, but did not analyze the concurrently recorded neural data (Murali & Händel, 2022)..

6.2.1 Participants

Twenty-three fluent German speakers (4 males) between 18 and 35 years were recruited from a local participants' pool via the SONA system (https://www.sona-systems.com/). The experiment was conducted according to the European data protection law (DSGVO) and was approved for COVID-19 Hygiene regulations. All participants gave written informed consent before the start of the experiment and received monetary compensation for their participation.

6.2.2 Task

The Guillford's AUT (Guilford, 1967) was used to assess divergent thinking. A total of 8 German words describing everyday objects were used for this purpose: bandage, brick, chair, desk, frying pan, garbage bag, lipstick, newspaper (translated to German). The task was to come up with as many alternate uses as possible for the object. MATLAB 2015a, with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) was used to run the experiment.

A within subject design was conducted with 4 conditions: free walking, restricted walking, free sitting and restricted sitting. During **free walking**, subjects walked around a room choosing their own path freely. In the **restricted walking** condition, they had to walk in a straight path, back and forth from wall to wall in the center of the room. A horizontal mark depicted the width of the path. During **free sitting**, the participants sat comfortably on a stationary non-rotating armchair with a solid non-moving back and no wheels. They were explicitly told that they were allowed to sit freely and should only remained seated. For all subjects the position of the chair was against one of the walls of the room such that the person would face the room and not the blank wall. Lastly, during **restricted sitting**, they sat in the same chair 50 cm from a computer screen and had to fixate on a fixation cross at the center

of the screen. The position of the chair and laptop was always the same for all subjects (Fig ***23***).

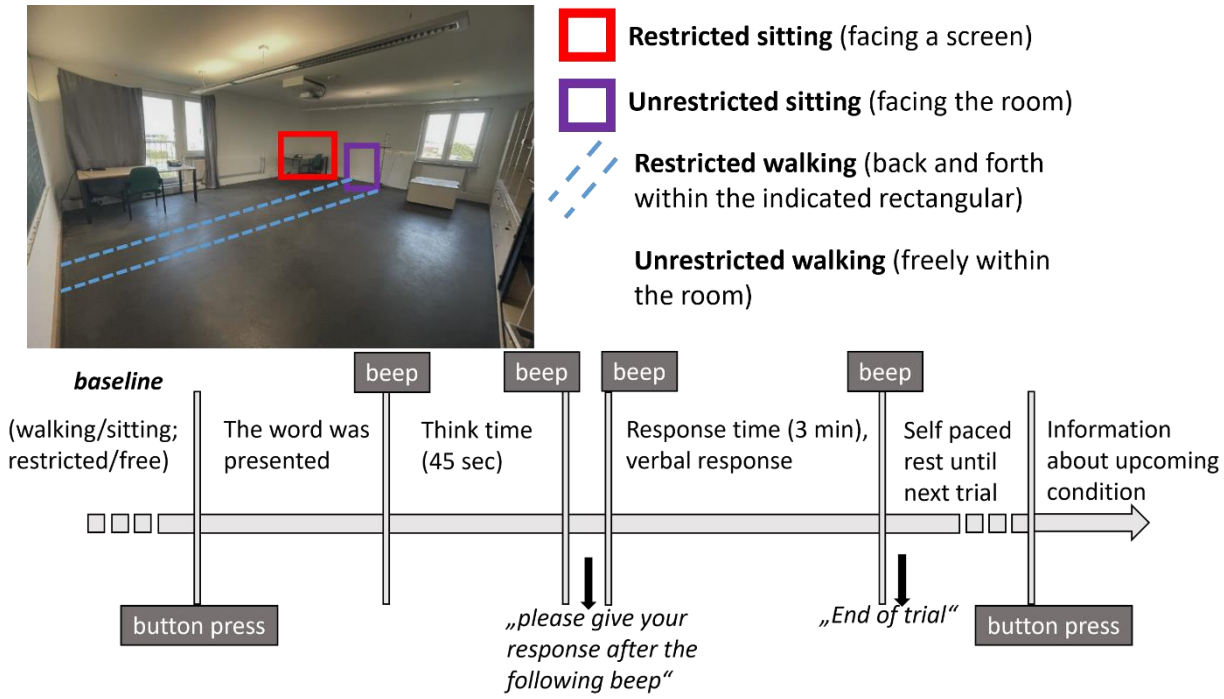

Fig. 23. Experimental setup and task. Four different movement conditions (restricted sitting, unrestricted sitting, restricted walking, unrestricted walking; randomly assigned) were executed in a 5x6 m^2 room. After having comfortably executed the movement condition for some time, subjects started the trial with a button press. A word (representing an object) was presented via speakers and subjects had 45 seconds to think about the answers followed by a 3 min period to verbally report as many alternate uses for the object they could think of. All instructions were given via automated auditory output and beeps.

At the start of the experiment, a randomization was applied, such that a random order for the conditions and words was generated. An automated voice informed the subject at the beginning of each condition about the upcoming required movement. The subject started the required movement and used a manual response (model: K-RB1-4; The Black Box ToolKit Ltd, UK) to indicate when they were ready to begin a trial. The baseline measurements were taken during this time before the button press. After the button press, a word was presented via the in-built speakers of the laptop using a text-to-audio function in MATLAB. Subjects had

then 45 seconds to think about the answers and 3 min to give their answers verbally using an external clip-on microphone.

Subjects were instructed that they could give as many responses as possible, but should not give non-use responses, such as “throw away”. At the end of the (3 min) response time, participants were allowed to take a break with no minimum or maximum limit in length. Subjects pressed a key when ready for the next trial or condition. The experimenter monitored the participant in order to detect obvious violations of the task requirements regarding movement or restriction.

For each movement condition, two consecutive trials (one words each) were presented, resulting in 8 trials but only 4 baselines. The verbally given responses were saved as a raw audio (wav) format. The experiment was conducted in a room of approximately 5*6m^2 and took about an hour to complete (excluding EEG setup preparation).

6.2.3 Data recording

EEG data were collected with a Smarting mobile EEG system (mBrainTrain LLC, Serbia), with a sampling rate of 500 Hz and data was transmitted via Bluetooth from the amplifier (that was attached to the cap) to the recording laptop. We used a passive 24-electrodes EEG cap which had a custom layout: 6 electrodes (3 electrodes for each eye: one below and one above the eye, one to the outer canthus) were used for electrooculogram (EOG) recording, which were included in the independent component analysis (ICA) for removing eye movement artefacts. Two further electrodes were placed on each earlobe for possible re-referencing. The remaining 16 electrodes were EEG recording electrodes. For online reference, the common mode sense active electrode placed between Fz and Cz was used.

6.3 Data analysis

6.3.1 Behavioural analysis

We used the fluency and flexibility scores of the AUT. For scoring, we first rejected responses that were 1) repetitive (a repetition of a previous use); 2) implausible (given the objects properties, e.g., pen used as a skirt) or 3) a non-use (e.g. throw in the garbage).

Repetitions were excluded to avoid high fluency scores based on repetitive ideas only (Zhang et al., 2020). Please see the previous study (Murali & Händel, 2022) for more details on the criteria. For the remaining responses, the fluency score was defined as the total number of correct responses and the flexibility score was the number of different categories in the responses.

6.3.2 EEG pre-processing and power calculation

The continuous EEG data for each participant was first pre-processed using the Fieldtrip toolbox (Oostenveld et al., 2011) and in-house scripts using Matlab (The MathWorks Inc., USA). A low-pass filter with a cut-off frequency of 100 Hz and a high-pass filter with a cut-off frequency at 1 Hz were applied (one-pass, zero-phase, firws). A band-stop filter with a cut-off between [49.5 50.5] Hz was applied to remove the 50 Hz power line noise. A principal component analysis was performed to reduce the spatial dimensionality of the EEG data to 16, which was followed by an ICA to correct for eye movements, heartbeat, and muscle related artefacts. An average of 3.78 artefact components (*SD* = 1.00; out of the total 16 components) were rejected.

The pre-processed EEG data was segmented into “trials”, i.e. for each word, data segments of constant length of 1 s with an overlap of 50 % were defined. Multi-taper fast Fourier Transform (FFT) was used to compute the power spectrum for each segment and each frequency between [1 100] Hz (in steps of 1 Hz, spectra for all individual segments were kept). Next, the segmented power spectrum was reformatted into a regular time-frequency representation. A log transformation was applied to reduce the variance among participants.

6.3.3 Alpha power

Alpha power between [8 14] Hz over the occipital electrodes O1 and O2 were analyzed choosing the same frequency band as in previous walking-related studies (Chen et al., 2022). We used the relative alpha power as it allowed us to get rid of the movement induced upward shift observed in all frequencies, following an approach used in other movement related studies (Cao et al., 2015; Holt et al., 2019; Hu et al., 2012). To calculate the relative power, the power was summed across the frequency range ([1 30] Hz). Then, the power of each

frequency was divided by the sum and multiplied with 100, resulting in a percentage representing the weight of each frequency bin in the spectrum. A three-way (movement: walk vs. sit; restriction: free vs. restricted; task phases: baseline vs. think time) repeated-measures ANOVA was performed with the relative power to investigate the effect of movement and restriction.

We evaluated the topography of alpha power contrast between restriction conditions applying a non-parametric cluster-based permutation test (Maris & Oostenveld, 2007). First, the relative alpha power (normalized, [8 14] Hz) during the think time was averaged over the two movement conditions (walk and sit) and a two-sided paired t-test between the free and restricted condition was applied to each electrode data. T-values with a cluster-alpha value of below 0.05 would form a cluster with neighboring electrode t-values given that their cluster-alpha value was also below 0.05. The spatial neighborhood of each electrode was defined as all electrodes within a 2 cm range. The cluster with the maximum summed t-value was taken as original value. Then, a cluster-based permutation test between the two restriction conditions (free vs. restricted) was performed. Then, cluster t-values following the same logic were calculated based on 1000 randomizations of the data. The original comparison was considered significant if its t-value was larger than 5% of the randomized t-values.

6.3.4 Alpha lateralisation

Since the relative alpha power was calculated as the weight of each frequency bin in the whole (1-30 Hz) spectrum for each electrode independently, the difference between electrodes cannot be revealed. Accordingly, alpha lateralisation was calculated with the non-normalized band alpha power (10-14 Hz). The alpha band corresponds to the one used in previous studies on the relationship between alpha lateralisation and creative ideation (Fink et al., 2011; D. Schwab et al., 2014). We calculated the alpha lateralisation for frontal, central, partial and occipital cortical areas based on the left electrodes (F3, C3, P7, P3, O1) and right electrodes (F4, C4, P8, P4, O2) using the following formula:

$$\text{Alpha lateralisation} = \frac{\text{alpha power (right electrode)} - \text{alpha power (left electrode)}}{\text{abs (alpha power (right electrode))} + \text{abs (alpha power (left electrode))}}$$

Positive values therefore mean stronger alpha power in the right hemisphere.

To find out which area shows a significant difference in alpha lateralisation between the free and restricted condition, a non-parametric cluster-based permutation test (Maris & Oostenveld, 2007) was performed across five cortical areas. As already describe above, the five alpha lateralisation values during the think time were averaged over the two movement conditions (walk & sit) and a two-sided paired t-test was calculated between free and restricted. Only t-values with a cluster-alpha value below 0.1 were used for the generation of spatial clusters. Neighboring electrodes were manually defined based on their location (below a distance of 2 cm). Note that, given the low total number of lateralisation, we only required 1 adjacent significant neighboring sample for a significant sample to be included in a cluster. The cluster with the maximum summed t-value was taken as original value. Second, cluster t-values following the same logic were calculated based on 1000 randomizations. The original comparison was considered significant if the t-value was larger than 5% of the randomized t-values.

A three-way (movement: walk vs. sit; restriction: free vs. restricted; task phases: baseline vs. think time) repeated-measures ANOVA was performed with the alpha lateralisation from the electrodes in the significant cluster.

6.3.5 Correlation analysis

To measure the relationship between alpha power/alpha lateralisation (during the think time) and behavioural performance (measured as fluency and flexibility score), within-participant correlations were performed. Two participants were not included because of missing behavioural data (one only had 1 trial for each condition, another participant had behavioural scores of zero). With the remaining participants (n = 21), the Spearman's rho (rs) was calculated between the relevant measures (e.g. alpha power and fluency score) over the 8 testing sessions (i.e. 2 movement states x 2 restrictions x 2 trials during think time). The

resulting 21 rho values (Fisher's z-transformed) were subject to a one sample t-test against 0 to check for a statistically significant trend in the relationship between alpha power and behavioural measures. A significant within-participant correlation was assumed given a t-test result of $p < 0.05$.

Additionally, a within-participant correlation between the alpha lateralisation and the alpha power was performed using the data from the 8 think times. The t-test between rho values and 0 was based on 22 participants (here only the participant who had only 1 trial for each condition was excluded, the participant with missing behavioural data was included).

6.4 Results

6.4.1 Previous behavioural results

Please see Murali and Händel (2022), section 4.5.1 figure 5. For convenience we repeat the main findings: a repeated-measures two-factor ANOVA for the factors movement (walk vs sit) and restriction (free movement vs. restricted movement) was applied for both fluency and flexibility scores. The main results, as described in Murali and Händel (2022), showed for fluency a significant effect of restriction, with free leading to higher fluency score; and a very close to significant p-value ($p = 0.05$) for movement, e.g, higher score during walking. There was no significant interaction. For flexibility, there was a significant effect of restriction, with free leading to higher score; and a very close to significant p-value ($p = 0.07$) for movement; No significant interaction was found.

6.4.2 Reduced alpha power was linked to higher behavioural scores

As we predicted that alpha power is smaller during walking compared to sitting and during the free compared to the restricted conditions independent of the task, a three-way (movement: walk vs. sit; restriction: free vs. restricted; task phases: baseline vs. think time) repeated-measures ANOVA was performed with the relative power. The results showed a main effect of movement ($F(1, 22) = 8.75$, $p = 0.01$), with lower alpha power during walking ($M = 3.42$, $SD = 0.76$) than sitting ($M = 3.90$, $SD = 1.04$). The main effect of restriction was also significant ($F(1, 22) = 13.76$, $p = 0.001$), with the free condition ($M = 3.47$, $SD = 0.76$) showing a lower alpha power compared to the restricted condition ($M = 3.85$, $SD = 0.96$). No other

main effect or interaction was statistically significant. The relative power is shown separately for think time and baseline for each condition in Fig ***24a/b*.**

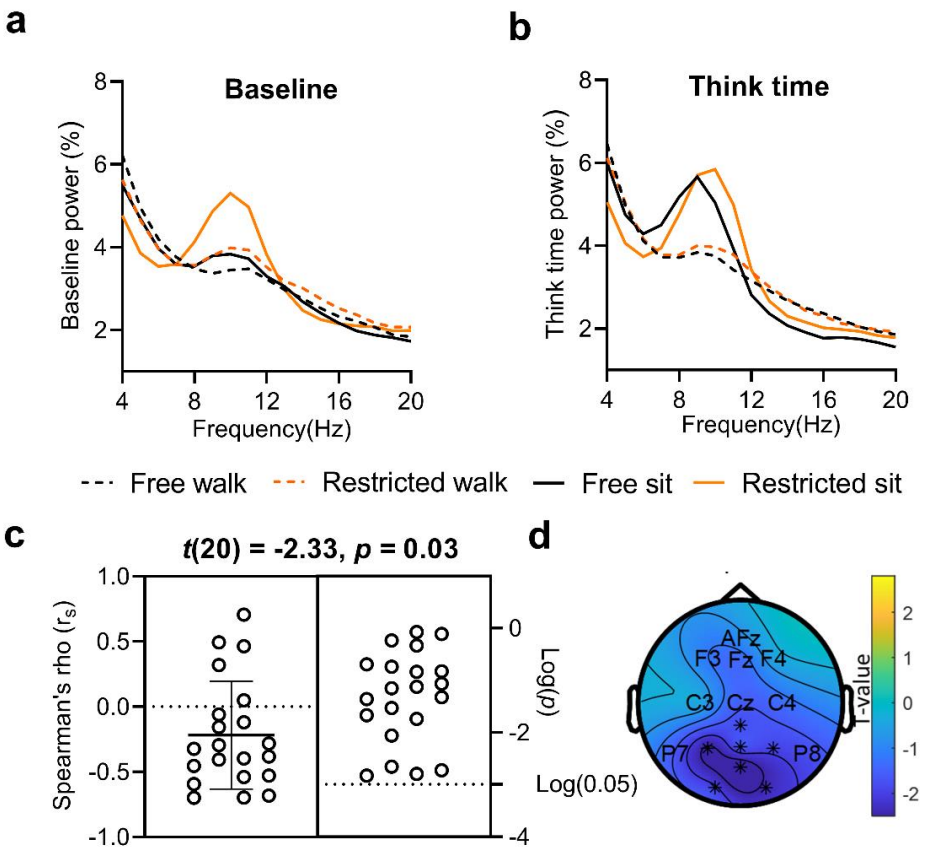

***Fig. 24**. Alpha power results. The power spectrum of the alpha power ([8-14] Hz, occipital O1 and O2 electrodes) for free walking (black broken line), restricted walking (orange broken line), free sitting (black solid line) and restricted sitting (orange solid line) during baseline (**a**) and think time (**b**). (**c**) Within each participant (n = 21), the correlation between the relative alpha power and fluency score was calculated based on the 8 trials (2 movements × 2 restrictions × 2 words). The significant one-sample t-test over the Spearman's rho values (r_s) (z-transformed; n = 21) indicates a relationship between the relative alpha power and the fluency score. Spearman's rho data is plotted on the left side while the p-values are plotted on a log scale on the right side. Each circle represents a participant. (**d**) Results of the cluster permutation test for the comparison of alpha power during think time of the free vs. restricted condition (averaged over walking and sitting). The topographical map shows the t-value distribution. Clusters of electrodes which showed a significant difference between the two conditions are highlighted with *.*

To test our prediction that lower alpha power was related to better performance in the divergent thinking task, the relation between think time alpha power and fluency/flexibility scores was tested separately via a within-participant correlation. We found a significant trend of the Spearman's rho values to be negative (t-test between each participant's *r* value with zero) indicating that a lower alpha power goes hand in hand with a higher fluency score (t-test between each participant's *r* value with zero: $t(20) = -2.33$, $p = 0.03$, figure ***24c***) and, marginally significant, with a higher flexibility score ($t(20) = -1.82$, $p = 0.08$).

A cluster-based permutation test (spatial clusters over the electrodes) between the two restriction conditions (free vs. restricted) showed that the alpha power difference between free and restricted conditions had an occipital focus; the only significant cluster ($p = 0.003$) was found over the occipital cortex (CPz, Pz, P3, P4, POz, O1, O2), see Fig ***24d***.

6.4.3 The free movement condition led to a higher alpha asymmetry

Since the normalized alpha power was calculated as the weighted power of each frequency bin on the whole spectrum (1-30 Hz) for each electrode separately, the difference between electrodes cannot be revealed analyzing the relative alpha power. Therefore, to compare the true hemispheric difference between experimental manipulations, the alpha lateralisation was calculated with the non-normalized upper band alpha power (10 -14 Hz), which previously had been reported as a marker of creative ideation (Benedek et al., 2011; Fink et al., 2009; Fink et al., 2011) A non-parametric cluster-based permutation statistical showed the lateralisation pairs P7-P8 and O1-O2 as forming the only significant cluster (figure ***25a***). Accordingly, we performed a three-way (movement: walk vs. sit; restriction: free vs. restricted; task phases: baseline vs. think time) repeated-measures ANOVA with the alpha lateralisation data based these electrode-pairs. A significant interaction between restriction and task phase was found ($F(1, 22) = 6.47$, $p = 0.02$), We additionally found a significant interaction between movement, restriction and task phase ($F(1, 22) = 6.25$, $p = 0.02$) (figure ***25b***). A following t-test showed that the alpha lateralisation was significantly stronger during the free condition than the restricted condition only during think time while sitting ($t(22) = 3.51$, $p = 0.008$, FDR corrected). A main effect of restriction was only close to significance ($F(1, 22) = 3.64$, $p = 0.07$), with alpha lateralisation during the free condition ($M = 0.06$, $SD = 0.24$)

being stronger than during the restricted condition (*M* = 0.02, *SD* = 0.22). No other effect was statistically significant.

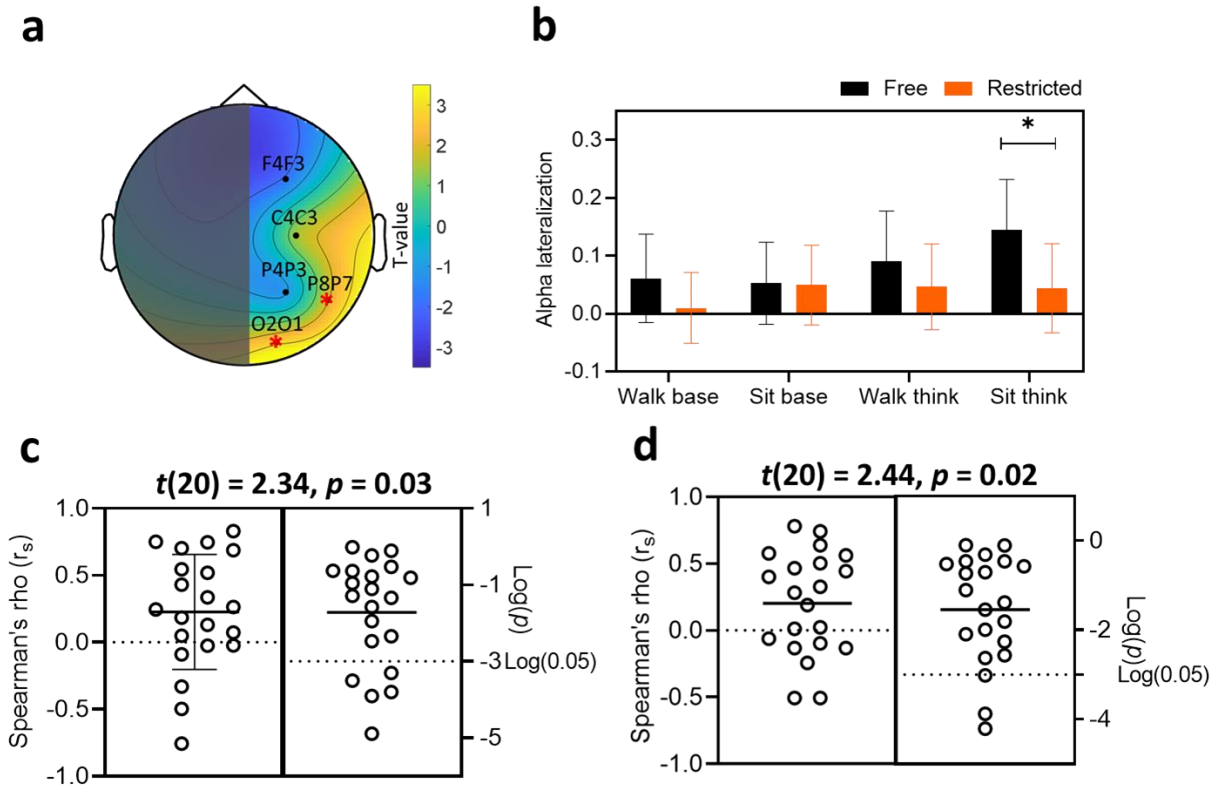

Fig. 25. Alpha lateralisation. (**a**) Topographical representation of the alpha lateralisation during the think time between the free and the restricted movement condition. Positive values mark higher alpha lateralisation during the free conditions. A significant cluster was only found in parieto-occipital electrode pairs (P7~P8, O1~O2) as marked with a red asterisk. (**b**) The lateralisation values in the upper alpha band ([10 14] Hz) are plotted separately for the task phase (think time, baseline) and the movement condition (walking, sitting, free, restricted). A more positive lateralisation value reflects stronger alpha power in the right electrode. A post-hoc t-test showed a significant difference between the free and restricted condition during think time while sitting. (**c**) The significant one-sample t-test between the Spearman's rho values (r_s) (z-transformed) and 0 (n = 20) indicates a relationship between the alpha lateralisation and the flexibility score. Spearman's rho data is plotted on the left side while the p-values are plotted on a log scale on the right side. Each circle represents a participant. (**d**) Same as **c** but with the fluency scores.

We then examined the relationship between the alpha lateralisation and divergent thinking task performance. To this end, a within-participant correlation between the think time alpha lateralisation and fluency/flexibility scores was performed separately for each subject. The Spearman's rho values from the subjects where then tested against zero. We found a significant trend of the Spearman's rho values to be positive (t-test between each participant's *r* value with zero: $t(20) = 2.34$ $p = 0.03$, figure ***25c***) indicating that a higher alpha lateralisation goes hand in hand with a higher flexibility score. When testing the fluency score, we again found a significant trend of the Spearman's rho values to be positive ($t(20) = 2.44$, $p = 0.02$, figure ***25d***).

A within-participant correlation between the occipital upper alpha band power and the alpha lateralisation values showed no significant correlation between the two neural markers ($t(21) = -1.61$, $p = 0.12$).

6.5 Discussion

The main aim of the work at hands was to understand the relation between alpha activity over occipital cortex and creativity by testing divergent thinking performance while measuring mobile EEG during different movement and restriction states. It had been show previously that walking reduces occipital alpha power (Cao et al., 2020). Additionally, it has been shown that free walking much more than restricted walking improves creativity (Murali & Händel, 2022). Accordingly, we tested if movement restriction had a correspondent in occipital alpha power and if this alpha power correlated with measures of creativity. Indeed, we found that alpha power was reduced not only during walking vs sitting but also during free vs restricted conditions. A significant alpha power difference due to restriction showed a focus over occipital cortex. Additionally, there was a negative relationship between occipital alpha power and performance in the divergent thinking task. These findings fall in line with the interpretation that alpha activity is related to certain aspects of creativity, particularly, that decreased alpha power over occipital cortex goes hand in hand with an improvement of the ability of divergent thinking.

However, we want to point out that behaviourally the restriction is more effective whereas alpha power is more strongly reduced due to walking. Similarly, it has been reported

that closing one's eyes increase AUT performance (Ritter et al., 2018) but at the same time eye closure leads to a most pronounced increase in alpha power (Berger, 1929). This indicates that alpha power effects cannot be generalized, and more work needs to be done to understand the complex underlying neural condition that boosts creativity.

Importantly, a correlation between a behavioural and neural phenomenon does not per se improve our understanding of the underlying process. However, in this case we find an indication of the mechanism based on the neural responses. A) given numerous previous findings that link the neural phenomenon of occipital alpha to attention, our findings present evidence that the relationship between creativity and alpha power is based on attention related processes. It is known that creativity is boosted by a defocusing of attention (Friedman et al., 2003) and alpha power over occipital cortex indicates the extent of the attentional focus (van Dijk et al., 2008). Further, alpha power modulated by walking seems related to the broadening of the focus of attention (Cao & Händel, 2019). Accordingly, we think that the possibility to perform unrestricted movements changes the attentional state of the participant by modulating alpha power over occipital cortex. B) While a behavioural effect can only be detected via a task/ response combination, neural activity can uncover general states which might influence task outcomes, temporally independent of the actual task. In our case, we found the same decrease in alpha power due to movement/movement restriction in the time in which the creative task was known or solved (think time) as well as independent of the task (baseline). This indeed suggests a state effect.

Overall, we propose that an unrestricted motor state broadens the focus of attention, accordingly decreasing the inhibition of large field visual processing. This change in attention is indicated by occipital alpha power. The reduced inhibition positively affects the generation of divergent ideas. However, even though the focus of alpha power modulation over occipital cortex suggests an emphasis on visual processes, we want to advise caution to prematurely limit this effect to vision particularly as we show that the alpha power modulation persists if task information is not presented visually.

Alpha power has been previously associated with creativity, and alpha lateralisation that has been shown to be correlated with creative test scores. Schwab and colleagues had reported a strong effect where the production of more original ideas was accompanied by

increasing hemispheric asymmetry (more alpha in the right than left hemisphere) with increasing duration of the idea generation period (Schwab et al., 2014). We could reproduce the direction of the alpha lateralisation and for the think time we confirmed the connection between alpha lateralisation and creativity scores by showing a significant tendency of individuals to perform better in an AUT task with increased lateralisation (corresponding to a positive correlation). However importantly, we found higher alpha lateralisation for restricted compared to free condition only to be significant during think time when sitting. This indicates that alpha lateralisation (at least during sitting) is not a state effect but specific for the time in which the ideas need to be created (think time). Please note that Schwab's setup required participants to sit in front of a screen and attend to visual information on the screen.

Further, we tested if the alpha lateralisation was connected to the described relative alpha power effect. While we did find the effects to be partly overlapping in electrodes, we found no indication that alpha power correlated with alpha lateralisation strength. This might be due to a power effect, however, the finding that alpha lateralisation showed no restriction related changes during baseline, but relative alpha power did show a modulation due to restriction during baseline, indicates two separate processes.

6.6 Conclusion

We find neurophysiological evidence that occipital alpha power, which is modulated due to movement and movement restriction, is positively related to the generation of divergent ideas. This alpha modulation was prevalent already during baseline, i.e. independent of the actual task, and therefore suggest a general movement induced change in attentional state. A second neural correlate of creativity, namely alpha lateralisation, was specific for the sitting condition and not correlated to the alpha state change due to movement/movement restriction. Overall, our work shows that movement such as walking, as well as missing movement restriction reduces the ongoing occipital alpha power. This reduced alpha power is an indicator of a changed state which is paralleled by increased creativity.

7. General discussion

An important goal of research on cognition is to understand how people process, perceive, and respond to objects in natural environments. As a fundamental body movement, natural walking serves as a gateway to understanding cognition during natural behaviour. This thesis project aimed to explore how natural walking changes occipital alpha oscillations and concurrently modulates cognitive processes. I first tested whether the modulation of occipital ongoing alpha power is independent of visual input (study 1). In the following four studies (study 2 – study 5), I investigated the influence of natural walking on different cognitive processes and sensory modalities while also assessing their functional connection to ongoing alpha power modulation.

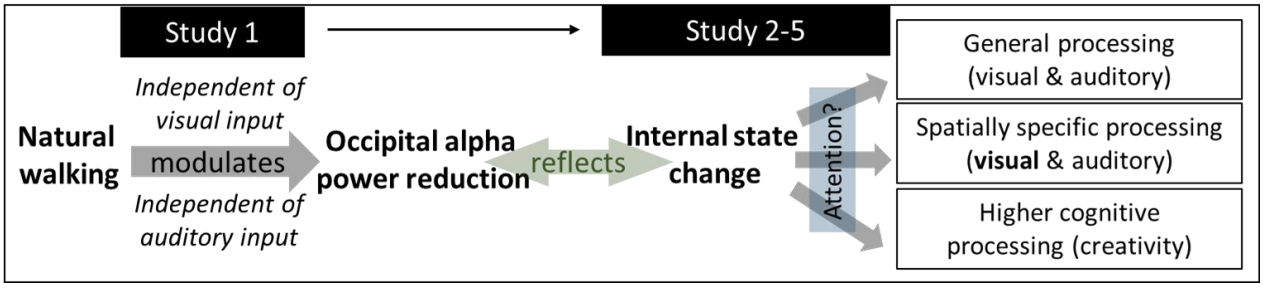

Figure 26. The overview of the thesis project. This project investigated how natural walking changes occipital alpha oscillations and concurrently modulates cognitive processes. The experimental work of this project showed that natural walking leads to a reduced ongoing occipital alpha power independent of visual input and auditory input changes (7.2). The alpha power modulation reflects a general change in the internal state, which could modulate various cognitive processes (7.3). Based on the findings from my studies, the modulations on cognition include i) general enhanced processing of visual and auditory input, independent of specific stimulus manipulations (7.3.1). ii) Spatially specific enhanced processing of peripheral visual and auditory input (7.3.2). iii) Higher cognitive processing, specifically a divergent thinking improvement (7.3.3). Attention is discussed as a potential mechanism of these findings (7.4).

The findings from studies 1-4 show that natural walking led to a reduced ongoing occipital alpha oscillation that was independent of visual and auditory input changes. This suggests that walking introduces a general change in internal state. The reduction on alpha

activity indeed predicted the walking induced enhancement of neural markers of temporally early visual processes and primary auditory responses during natural walking. This modulation was independent of specific stimulus manipulations. Through a separate process, natural walking induced a spatially specific modulation, specifically an enhancement in peripheral processing. Such spatially specific processing was dependent on the walking path. In study 5, the investigation into higher cognitive processes, particularly divergent thinking, revealed that the reduced ongoing alpha power could serve as an indicator of the modulation of divergent thinking during natural walking. Throughout this manifold work, I highlight the potential role of attention during natural walking. The overview of the current project can be seen in Figure ***26***.

In the following section, I will provide a summary of the results of each study.

7.1 Summary of the results

In study 1, I investigated the influence of natural walking on ongoing alpha oscillations in darkness and light. The results revealed a decreased alpha power over the occipital cortex during natural walking compared to standing, irrespective of the lighting conditions (Cao, Chen, & Händel, 2020). This study indicated that the reduced alpha power during natural walking was not caused by changed visual input. I also provided evidence that the modulation was not based on eye movements or electrode impedance. Given that alpha power has been functionally linked to inhibition, I interpreted the observed reduction as a disinhibition of the occipital cortex. This could suggest that natural walking enhanced visual processing and possibly any cognitive process that involves occipital cortical activity.

Using a visual discrimination task, study 2 was performed to examine the possible effects of natural walking across visual processing stages by assessing various neural markers during different movement states. The findings revealed an amplified early visual response (N1 component) during natural walking, while a later visual response (N2pc component) remained unaffected (Chen, Cao, & Haendel, 2022a). These results suggested that natural walking specifically leads to enhanced early sensory processes.

A follow-up study 3 further investigated the nature of the effect of movement state on early sensory processing and how it is linked to the modulation of ongoing alpha power (Chen, Cao, & Haendel, 2022b). The results replicated the walking-induced enhancement of the early ERPs and showed that this could be predicted by the walking-modulated pre-stimulus occipital alpha power. No evidence was found that the effect of natural walking on early ERPs was dependent on specific stimulus-related parameters (eccentricity, laterality, distractor presence). In contrast, walking also modulated the post-stimulus alpha power but this was dependent on stimulus-related parameters such as eccentricity. There was no evidence of a correlation between pre-stimulus and post-stimulus alpha power.

The results with modulations of early ERPs so far suggested that natural walking led to an enhancement in temporally early visual processes, which can be predicted by ongoing occipital alpha oscillation. In addition, there was a dissociable influence of natural walking on later visual process stages, favouring singular peripheral input.

In study 4, I turned to the auditory domain. I investigated the influence of stepping or natural walking in a particular path on ongoing occipital alpha oscillation, ASSR, and ASSR amplitude perturbation. The results showed that i) enhanced processing due to natural walking can be found in primary auditory brain activity; ii) the modulation of auditory processing was dependent on features of the walking path; and iii) the spatial preference for peripheral sensory processing as found in vision, was also present in audition.

In study 5, I lastly examined the modulation of ongoing alpha oscillation due to natural walking and its possible relation to higher cognitive processes, namely creative divergent thinking. The results showed that, again, the occipital ongoing alpha power was lower during natural walking compared to sitting but also during unrestricted compared to restricted movement conditions. The ongoing alpha power was further negatively correlated to the creativity scores. Also, alpha lateralisation during the think-time showed a relationship with creativity scores but did not correlate with the ongoing alpha power. These results suggested that movement as well as missing movement restriction reduced the ongoing occipital alpha power. The occipital alpha power reduction can be an indicator of a changed state that improved higher cognitive processes.

7.2 Natural walking reduces ongoing alpha activity independent of the visual and auditory input suggesting a general change in the internal state

Previous studies have shown a robust reduction of ongoing alpha power across the parieto-occipital cortex during body movements (Cao et al., 2020; Ehinger et al., 2014; Kuziek, Redman, Splinter, & Mathewson, 2018; Lin, Wang, Wei, & Jung, 2014; Nenna, Do, Protzak, & Gramann, 2020; Robles et al., 2021; Scanlon, Townsend, Cormier, Kuziek, & Mathewson, 2019; Shaw et al., 2018; Vaughn et al., 2021; Zink, Hunyadi, Huffel, & Vos, 2016). However, what causes the reduction of ongoing alpha, especially whether this is due to body movement or prevalent sensory input changes, remained unknown. In my project, I consistently observed a reduction in ongoing alpha power, most prominent in the occipital cortex, during natural walking compared to stationary states (standing or sitting) in all studies. This reduction occurred irrespective of the presence or absence of visual input or visual task and was unaffected by the parameters of the visual input. The reduction was also observed when auditory input changes were controlled between different movement states. Considering also the previous studies, my findings indicate that i) modulation of ongoing alpha oscillations due to natural walking does not depend on specific sensory input, rather, ii) it is the natural movement itself that drives the robust effect. In addition, iii) although the reduction is predominant in the occipital cortex (the visual processing centre), it can be predictive for sensory processing in both visual and non-visual domains. Those finding will be discussed in detail below.

The explanations of what caused the reduction of ongoing alpha due to body movement in previous studies were mainly based on assumptions without undergoing further testing. A specific interpretation can be seen in the study by Scanlon et al. (2019). In their study, they argued that the reduced parietal alpha power during outdoor cycling compared to sitting indoors was a result of the altered sensory input experienced between outdoor and indoor environments. However, they did not balance the body movement in each environment to consider the role of the motor output. A study by Vaughn et al. (2021) provided suggestive insights into the significance of body movement in affecting the occipital alpha oscillation. In the investigation by Vaughn et al. (2021), the occipital alpha power was compared between sitting, non-stationary cycling, and driving on the same outdoor single-

lane road. Two significant results should be highlighted. First, no significant difference in occipital alpha power was observed between sitting and driving. This suggested that mere changes in visual input during driving are insufficient to induce alterations in alpha oscillations. Second, a reduction in alpha power, mainly in the occipital cortex was found during non-stationary cycling compared to driving. Intriguingly, both cycling and driving involve similar changes in visual input, yet driving does not necessitate active bodily movement. These findings indicated that it is the coordinated engagement of the body, rather than changes in visual input that lead to the modulation of ongoing alpha power.

Another study worth discussing is that of Liang, Starrett, and Ekstrom (2018). They examined the alpha power between body movements, comparing conditions with eyes open versus eyes closed. Their results showed a decreased occipital alpha power during treadmill walking compared to standing only when participants opened their eyes. This result seems to be an indication that the visual input was the prerequisite for observing the modulation of ongoing alpha oscillation due to body movement. However, the absence of decreased alpha power during body movement with eyes closed could also be attributed to the overall increase in alpha power caused by the closure of the eyes. This increase in alpha power due to eye closure is a long confirmed effect (Barry & De Blasio, 2017; Berger, 1929; Liang et al., 2018; Webster & Ro, 2020; Wostmann, Schmitt, & Obleser, 2020). The authors themselves proposed an alternative explanation for their observation of reduced alpha power only when eyes are open. They assumed that this reduction might be caused by a decrease in physical relaxation when eyes are open during treadmill walking, given that occipital alpha is often considered an indicator of cortical idling (Pfurtscheller, Stancak, & Neuper, 1996). This interpretation, although attributing the reduction to cortical idling, highlighted role of body movement itself in modulating the occipital alpha oscillations. Nevertheless, it is necessary to include a condition that controls for visual input but excludes the factor or eye closure to understand what caused the occipital alpha modulation.

To investigate whether the modulation of alpha power is dependent of changes in visual input, I compared the alpha power difference between body movement states with the control of visual input changes with eyes always opened (Cao et al., 2020). The results showed decreased occipital ongoing alpha power due to natural walking in both light and darkness.

This suggested that the modulation of ongoing occipital alpha oscillation is not introduced by a change in visual input during natural walking. I also provided evidence that the modulation was not due to eye-related movement or movement-related electrode impedance change. Besides controlling the factor of visual input changes, I further showed that the reduction was independent of auditory input change. In my auditory experiment (study 4), the auditory input was played via a pair of inserted earphones, and the volume was adjusted to a level where it surpassed the threshold for perceiving external auditory input. Such an experimental setup ensured that auditory input remained unchanged regardless of the body movement. With consistent auditory input maintained between different body movements, a significant reduction of occipital alpha power due to natural walking was again observed. This further indicated that the reduction of occipital alpha power due to walking is independent of auditory input changes.

The finding that natural walking reduced ongoing alpha activity independent of the visual and auditory input changes already suggested that this is a modulation driven by the motor output. However importantly, my findings as well as evidence from other scholars indicated that it is natural body movements that demonstrate the strongest influence on occipital alpha power. Those natural body movement typically consists of a combination of motor actions using musculoskeletal system and ecologically relevant purpose, such as going from one location to another. For example, In Vaughn et al. (2021)'s study, reduced occipital alpha power was only observed during non-stationary cycling, but not reduced during driving and sitting. This suggested that the reduction of alpha power was associated with an active engagement of the entire body during movement. Mere passive movement from one location to another does not seem to induce a decrease in occipital alpha power. Similarly, Zink et al. (2016) demonstrated that the occipital alpha power was reduced during non-stationary cycling compared to sitting. Their stationary cycling, e.g. paddling, involving movement of only the legs and feet, did not result in a significantly reduced alpha power compared to sitting. Their findings implied that moving only a specific part of the body without fulfilling an ecological aim might be insufficient to change occipital alpha power. Indeed, in my study 4, although showing a noticeable trend, the alpha power was not significantly reduced during the stepping condition when compared to sitting. This again highlighted the importance of an ecological aim in the body movement in modulating the occipital alpha power, which was

similar to what was observed in Zink et al. (2016). In all my studies, the robust findings of an alpha power reduction were all based on natural walking, wherein individuals use their body's musculoskeletal system to travel from one place to another (study 1 – study 5). Such significant reduction was also observed in another study based on natural walking (Cao & Händel, 2019). Certainly, also body movements such as treadmill walking and electric skateboarding can result in a reduction of occipital alpha power (Kuziek et al., 2018; Lin et al., 2014; Robles et al., 2021), however, I am proposing that it is natural movements, such as walking, that produce the most significant modulation of occipital alpha power.

What might be the mechanism of the occipital alpha power reduction due to natural walking? The changes of ongoing alpha oscillation that is sensory input independent align with findings from previous animal studies. There were many reports of modulation of neural activity in the primary visual cortex (V1) by running speed during complete darkness in mice and primates (Dipoppa et al., 2018; Y. Fu et al., 2014; Keller, Bonhoeffer, & Hubener, 2012; Saleem, Ayaz, Jeffery, Harris, & Carandini, 2013). These findings suggested a shared mechanism through which body movement influences neuronal responses. Regarding the possible mechanism, animal studies from Pakan et al. (2016) and Y. Fu et al. (2014) have suggested that the change in disinhibitory circuits during locomotion might at least partly account for the modulation of such primary visual cortex modulation in darkness. Our finding of a reduction in alpha oscillations, an activity that is likely related to inhibition and negatively correlated with firing rate (Haegens, Nacher, Luna, Romo, & Jensen, 2011), indicated that the body movement is also likely to influence the alpha power through an inhibition mechanism. Accordingly, the reduced ongoing occipital alpha oscillation due to natural walking might mark a state of decreased inhibition of sensory input.

The reduced alpha power was localized in the occipital cortex, which is primarily responsible for visual processing. Does the observed reduction in inhibition, as indicated by changes in occipital alpha power, exclusively impact visual processing? To address this question, I explored whether the influence of natural walking extends beyond visual sensory processing testing various cognitive processes. Indeed, the modulation of ongoing occipital alpha power can predict many cognitive processes beyond visual sensory processing. A comprehensive discussion of how walking influences sensory processing will be presented in

the upcoming section (7.3). In short, I established the link between the modulation of ongoing alpha power and sensory processing in of visual input (Chen et al., 2022b). Importantly, my study also showed that the decrease in occipital alpha power serves as a predictor for non-visual sensory processing in audition. Specifically, in study 4, with prevalent auditory stimulus presented, I demonstrated a robust link between the reduced occipital alpha and neural indicators of auditory sensory processing (ASSR and auditory evoked P1 component). This auditory effect adds that the changed sensory processing, marked by the alpha power reduction, is not a result of interaction within the visual domain. Essentially, considering the constant and predictable changes in visual input during natural walking, any conceivable impact on stimulus-related visual processing might arise from the interplay between those anticipated changes and stimulus-related visual inputs. However, the unaffected association between alpha oscillation and neural markers of sensory processing in the auditory domain would largely exclude this interaction possibility. Finally yet importantly, alpha modulation can predict higher cognitive processing such as divergent thinking (study 5). All those findings suggested a general change in the internal state reflected by the modulation of ongoing occipital alpha oscillation.

7.3. How the walking induced state change influences cognitive processes

7.3.1 Feature independent modulation of sensory processing due to natural walking

The reduction in ongoing occipital alpha oscillation due to natural walking described in study 1 (Cao et al., 2020) led to the assumption that the reduced alpha power reflected a state of decreased inhibition. If this would be the case, one expect that the walking induced occipital alpha power change is paralleled by a change in sensory processing. Based on the findings in my studies, enhanced sensory processing was indicated by a walking induced enhancement of neural signals related to temporally early visual processes (study 2-3) as well as primary auditory responses (study 4). Such modulation due to natural walking was independent of the stimulus-related manipulations in the given tasks. Accordingly, I refer to this modulation as 'feature-independent modulation of sensory processing' (also simply mentioned as general sensory processing in the following discussion). I conducted further investigations into the link between the modulation of early sensory processes, ongoing occipital alpha power, and its link to behavioural outcomes.

Enhanced early sensory processes

A feature independent modulation on early ERPs due to body movement was previously reported only in the auditory tasks. For example, using an auditory oddball task, Scanlon et al. (2019) reported an enhanced early auditory evoked N1 component amplitude during outdoor non-stationary cycling compared to sitting indoors. The enhanced N1 component during non-stationary cycling was independent of the stimulus-related manipulations, e.g. target or non-target. Vaughn et al. (2021) examined the neural marker known as the MMN component which was calculated subtracting the standard ERP from the oddball ERP. They found that the MMN component amplitude was larger during non-stationary cycling compared to both driving and sitting. This finding could be considered as evidence of an enhancement of temporally early auditory processes. In vision, the evidence of modulation on feature independent temporally early sensory processes is lacking. On the contrary, Bullock, Cecotti, and Giesbrecht (2015) observed an enhanced visual P1 component amplitude during stationary cycling compared to the resting state in a visual oddball task but only for standard non-target trials. Dodwell, Liesefeld, Conci, Muller, and Tollner (2021) showed an enhancement of the early Ppc component to be exclusively elicited by the distractor.

In my project, I tested how natural walking modulates the early visual ERPs in visual discrimination tasks compared to standing. Study 2 showed that natural walking led to an amplification of the early N1 component, the first major negative component after stimulus onset. Previous studies have suggested the primary visual cortex (V1) as the neural substrate responsible for the first negative component (Di Russo et al., 2005; Perfetti et al., 2007). However, in these studies, the N1 component occurred significantly earlier, typically within 100 ms after stimulus onset. While there is the possibility that the N1 component in my studies also has a neural generator in V1, I refrain from making further assumptions regarding whether the N1 component (peaking around 150 ms) in my study is the primary cortical response. Rather, my interpretation mainly focused on its temporal earliness in comparison to the modulation of later ERPs. Accordingly, the enhanced early ERP amplitude due to natural walking is interpreted as indicative of enhanced temporally early visual processes (Chen et al., 2022a). Such enhancement due to natural walking was independent of target locations. In the

follow-up study 3, additional manipulations of stimulus-related parameters (distractor presence and eccentricity) were included. I found that the modulation of early visual ERP amplitude due to natural walking was not dependent on those stimulus-related parameters (Chen et al., 2022b). This study provided further evidence of the influence of natural walking on temporally early visual processes independent of task-related parameters.

I further tested the influence of natural walking on early sensory processes in audition. To this end, I examined the impact of natural walking on an entrained auditory response using ASSR in study 4. The ASSR is an electrophysiological measure of brain activity that reflects the entrainment of neural oscillations to a rhythmic auditory stimulus (Galambos, Makeig, & Talmachoff, 1981; Picton, Dimitrijevic, & John, 2002; Picton, van Roon, & John, 2009). Many previous studies have identified the cortical sources of the ASSR within the primary auditory cortex (A1) with magnetoencephalography (MEG) (Herdman et al., 2003; Ross, Herdman, & Pantev, 2005a; Teale et al., 2008). ASSR has further been utilized as an indicator of hearing ability in hearing tests and in the assessment of sensory processing dysfunction in clinical settings (Picton, Dimitrijevic, Perez-Abalo, & Van Roon, 2005; Sugiyama et al., 2021). In my study, a stronger ASSR power, was found during walking compared to standing. This primary auditory response modulation could reflect again an enhanced early sensory processing due to walking compared to standing. The focus of the term 'early,' could represent a hierarchical early processing, given that the modulation was within the primary cortical response. To be noted, at the same time, a correlation between the increased ASSR power and the heightened early ongoing auditory stimulus-induced temporally early P1 component due to natural walking was found. This suggested that the enhanced processing due to natural walking in primary auditory brain activity might concurrently manifest as a temporally early effect. Importantly, in my study, the enhanced primary auditory brain activity was presented with control of auditory stimulus between different movements. Such enhanced primary auditory responses due to natural walking have two implications: First, it excluded the possibility that the sensory processing enhancement was based on a low-level interaction within the visual domain. The entrainment auditory responses cannot be modulated by the predictions in visual input changes, e.g. general continuous and predictable changes in vision during walking. Second, the enhanced early sensory processes is not due to motor output. For instance, during walking in the pre-defined path, one would look to a certain direction (based

on visual prediction), therefore turn their head and likely to change the auditory input by moving the ears. This possibility is excluded as the auditory source is fixed to the head in my experiments. Overall, my findings strongly suggest a more general effect of natural walking on sensory processing due to an internal state change.

Consistent with what I discussed above regarding the importance of natural walking in modulating occipital alpha oscillation, current evidence also indicated that natural body movement is an important factor for revealing a maximum modulation on early sensory processes. In those studies which demonstrated enhanced temporally early sensory processes, the movement types (i.e. the walking condition in my studies, and the outdoor non-stationary cycling conducted by Malcolm, Foxe, Butler, Molholm, and De Sanctis (2018) and Vaughn et al. (2021) can all be considered natural body movements. As I mentioned in previous section (7.2), the natural movement refers to the movement consists of a combination of motor actions individuals using musculoskeletal system and ecologically relevant purpose, such as going from one location to another. Passively moving the body without motor actions, e.g. the driving condition in the study by Vaughn et al. (2021) cannot lead to an enhanced early MMN component compared to sitting. In fact, in my study 4, a significant difference in ASSR power between natural walking and stepping was observed (study 4). Such difference provided further evidence supporting the role of natural body movement in demonstrating the strongest sensory processing enhancement. The emphasis on natural body movement in both occipital alpha oscillation reduction and neural markers of early sensory processes potentially indicated a close relationship between these two modulations.

The link between enhanced early sensory processes to the modulation of alpha oscillation

Across all my studies, I established the link between the feature independent modulation of sensory processing due to natural walking and the modulation of occipital ongoing alpha power in both vision and audition. The idea that the modulation of ongoing alpha oscillation due to body movement is associated with a change in general sensory processing has been suggested in some prior studies but which lacked experimental evidence (Ehinger et al., 2014; Scanlon et al., 2019; Vaughn et al., 2021). Very consistent with our findings, using an auditory oddball task, a study by Scanlon et al. (2019) reported a generally enhanced early N1

component amplitude and reduced ongoing alpha power (however in parietal cortex) during non-stationary cycling compared to stationarity. Also in a later study (Vaughn et al., 2021), the neural marker of a temporally early sensory processes named MMN component amplitude was reported to be larger during non-stationary cycling compared to both driving and sitting, and the occipital alpha power was smaller during non-stationary cycling compared to driving and sitting. However, neither of them further analysed the relationship between modulations of the alpha power and ERPs. Nevertheless, these results are quite in line with my assumption of a functional link between the modulation of alpha power and neural markers of general sensory processing.

In my project, I provided evidence that the reduced occipital alpha oscillation due to body movement was indeed related to a change in neural markers of early sensory processes in the visual and the auditory domain: In the visual experiment (study 3), the pre-stimulus alpha power predicted the strength of visual processing indexed by the early ERPs (Chen et al., 2022b). In the auditory experiment, the occipital ongoing alpha modulation predicted the strength of early auditory processing indexed by the ASSR power (study 4). Additionally, the enhanced P1 component induced by the auditory tone was also significantly correlated with the occipital ongoing alpha power modulation due to natural walking. These correlations support the idea that walking influences the neural responses associated with general sensory processing likely via a change in ongoing alpha power. Specifically, concerning the results of the auditory experiments, two significant implications arise. Firstly, as elaborated earlier, the changed primary auditory responses due to natural walking effectively ruled out any direct influence from the visual realm. Secondly, even though the alteration in alpha power induced by natural walking consistently centred in the occipital cortex, my studies provided compelling evidence that such alpha modulation is predictive of sensory processing changes extending beyond the visual domain.

Why can a modulation of oscillations in the primary visual cortex predict sensory processing in the auditory domain? Animal studies have shown that sound can induce changes in V1 visual responses (Ibrahim et al., 2016; Williams, Angeloni, & Geffen, 2023), potentially suggesting a broader role for the primary visual cortex in integrating and processing sensory information from both vision and audition. In humans, it is possible that

the visual cortex does more than just visual processing and therefore activity changes in the visual cortex can change non-visual processes. Attention might serve as a related and more general mechanism through which activity changes in the visual cortex can change non-visual processes. However, one must remain careful as it could either mean that visual processes and their inhibition affect non-visual tasks because vision is so dominant in humans, or that a general attentional process is coordinated in the visual cortex. This question cannot be answered based on my current experiments. Another possibility is that the change in occipital alpha power and early sensory processing are both caused by natural walking, however, the modulation of alpha power does not directly cause the shift in sensory processing. For example, it is possible to employ neuroimaging techniques such as Magnetoencephalography (MEG) that enable the observation of the temporal sequence of events in future work and conduct analyses like Granger causality analysis to delve into causation. In general, my current experiments are limited in their ability to address the question of why a modulation of oscillations in the primary visual cortex can predict sensory processing in the auditory domain. Nonetheless, this is an intriguing question that warrants further investigation.

The link between enhanced early sensory processes to behavioural outcome

Despite an enhancement of early cortical response, my results showed that the enhanced temporally early sensory processes demonstrated only a partial association with behavioural outcomes. In my visual experiment (study 3), the pre-stimulus alpha power was only correlated with reaction time, but not with d' (a measure of discriminability). The results suggested that the modulation of ongoing alpha activity and the enhanced sensory processing due to natural walking was only associated with perceptual changes reflected by reaction time. This means that enhanced early sensory processing does not necessarily lead to an improvement in every aspect of behavioural task performance. Such exclusive link to reaction time might be related to some perceptual changes such as visual awareness change and will be discussed later (6.3.5). It should be noted that the perceptual changes reflected by reaction time changes due to body movement aren't always an absolute improvement. Instead, it can lead to elevated reaction time levels compared to accuracy-related performance. For instance, in Bullock et al.'s (2015) visual oddball study, a larger P1 component was found during low-intensity stationary cycling, indicating an improved temporally early sensory

processing. Their results showed a similar accuracy but a faster reaction time trend during this low-intensity cycling. It is possible that when body movement effectively maintains a comparable detection rate to the stationary state, the changes associated with improved temporally early sensory processing have the potential to enhance reaction times. In the task I conducted, walking led to a decreased d' compared to standing. However, certain specific perceptual changes potentially improved reaction time and aligned it with the same level observed during standing. In summary, these findings suggested that the early sensory processing changes due to walking potentially affect reaction time, while not necessarily changing objective detection or discrimination performance.

Indeed, according to the information processing model (Simon, 1979), a lot of processes are happening temporally later in cognitive task, and those later processes could also affect the behavioural outcome. Even though walking enhances the temporally early sensory processes, there are still some comparatively later processes that are specific to task features that might be differently influenced. For example, Bullock et al. (2015) found that the early P1 component amplitude was larger during low-intensity cycling compared to rest with standard trials in their visual oddball task, but they did not find any modulation on later P3 (both P3a and P3b, evoked by distractor and target separately) amplitude by cycling. Their latency analysis results, specifically with the target, also indicated a lower P1 amplitude during low-intensity cycling but did not show any difference between P3 latency. In addition, high intensity cycling led to the largest P1 latency but the smallest P3 latency (although not significant). In another study by Dodwell et al. (2021), when analysing the ERP induced by lateral distractor using a singleton task paradigm, moderate cycling led to a stronger early Ppc component which was established to be pre-attentive and temporally early cortical responses but no difference was observed with the later distractor-suppression related Pd component. Their results indicated that body movement could modulate multiple stages of information processing in different ways. In my study 2, despite an enhanced N1 component amplitude during natural walking, I found that neither the later N2pc component, a well-established neural marker of selective attention (Luck, 2012), not the later alpha lateralisation that correlated with the N2pc component, were modulated by natural walking. Additionally, in study 3, I extended the analysis to reveal distinct effects across processing stages by examining the modulation of various neuronal signals (early ERPs and later stimulus-induced

alpha power) in relation to pre-stimulus ongoing alpha. I also explored how the different modulations of natural walking were dependent on stimulus-related parameters. The finding in my study indicated generally two influences by natural walking: one was a temporally early modulation that was independent of specific task-related input, and another was a later task stimulus dependent modulation. This study provided further evidence of the different effects of natural walking across processing stages (Chen et al., 2022b).

The results from my studies showed that the behavioural outcome was mainly based on how temporally later processes were modulated. Previous studies have shown that early ERPs such as P1 and N1 mark early visual processing of sensory input. Those components were found to increase in amplitude when visual stimuli were presented at an attended location compared to a non-attended location using spatial cueing paradigms (Eimer, 1999; Eimer & Schroger, 1998; S. Fu, Greenwood, & Parasuraman, 2005). However, these early ERPs were also shown to be associated with imprecise and coarse feature encoding of the specific stimulus feature (Mazza, Pagano, & Caramazza, 2013; Rolke, Festl, & Seibold, 2016), and weakly correlated with behaviour. Late components, on the other hand, such as the lateralised N2pc component, are generally thought to be related to specific cognitive target processing that is significantly related to discrimination performance (for a review, see Luck, 2012). In my study, the N2pc component was co-modulated with behavioural performance as well as with another neural hallmark of attentional processes, namely alpha lateralisation. Additionally, I found a correlation between the N2pc component and the alpha modulation index. A co-modulation of the N2pc component and alpha lateralisation strength was expected if both mark an attention-related later discrimination-related cognitive process, which would be more strongly associated with behavioural performance. Indeed, I found comparable behavioural performance between standing and walking as shown with the N2pc component and alpha lateralisation (Chen et al., 2022a). In study 4, the smaller modulation of stimulus-induced alpha power, was also consistent with the lower d' observed during natural walking (Chen et al., 2022b). Similarly, Bullock et al. (2015) found no difference between later P3 component amplitude between stationary cycling and resting state but reduced distractor-induced P3 latency. Interestingly, their behavioural findings showed no accuracy difference between cycling and resting but only faster reaction time during cycling. This behavioural pattern appeared to align with the modulation observed in the later P3

component, where latency appeared to be more closely linked to alterations in processing speed. In summary, considering the collective findings from these studies, it is evident that natural walking influences various stages of visual processing. The behavioural performance seemed to be more strongly influenced by later stage processing.

Overall, the findings from my visual and auditory studies indicated that natural walking led to an enhancement in temporally early visual processes and primary auditory brain activity, which can be predicted by the walking-induced change in ongoing alpha. This suggested a change in internal state due to natural walking which affects basic early sensory processes beyond vision in a rather general way. However this influence was only weakly associated with behavioural outcomes.

7.3.2 Spatially specific modulation of sensory processing due to natural walking

In addition to the general modulation of sensory processing, body movement can also lead to a spatially specific improvement in sensory processing. More specifically, previous studies have shown that the peripheral visual input was more strongly processed during body movement. Cao and Händel (2019) found that the pre-target-induced SSVEP was more strongly modulated by the surrounding contrast during natural walking compared to standing, suggesting changed spatial processing during natural body movement. Indeed, they showed improved behavioural performance when detecting peripheral targets in the contrast change detection task during natural walking compared to standing. Evidence of an increased surround suppression effect during treadmill walking as compared to standing was also provided by Benjamin, Wailes-Newson, Ma-Wyatt, Baker, and Wade (2018) in a similar visual contrast detection task. A recent study, using a single-stimulus visual detection paradigm, showed that the latency of the second peak of the N1pc/N2pc complex was reduced during natural walking compared to stationary states only in the extrafoveal stimulus condition (Reiser, Arnau, Rinkenauer, & Wascher, 2022). This latency change was interpreted as a faster re-entrant processing of stimuli that have a diminished saliency during natural walking, which again suggests enhanced peripheral visual processing.

In my visual study, I manipulated the stimulus eccentricity in the visual discrimination task (Chen et al., 2022b). The behavioural results showed that, for no distractor condition, the d’

difference between standing and walking was larger for centre (1.3°) and smallest for a peripheral location with an eccentricity of 9°. This result was similar to the previous visual study which showed the largest peripheral enhancement effect due to natural walking with a similar visual angle, without the presentation of distractor (Cao & Händel, 2019). I did not observe a similar facilitation effect with an eccentricity of 16°, this was consistent with what Cao and Händel (2019) discussed, namely that there might be a limit to the distance of the peripheral visual field for receiving a processing advantage during natural walking. However, when comparing the d' between centre (1.3°) and peripheral (9°) processing when a distractor was presented, the d' difference between standing and walking was larger at the peripheral location compared to the centre location. Why the difference was larger for the peripheral stimulus condition than the centre condition when there was a distractor? One potential explanation is that natural walking enhanced overall peripheral processing, affecting both target and distractor stimuli. However, it is plausible that peripheral distractors exerted a more substantial impact on behavioural performance, leading to a further decline in performance compared to situations where the distractor was presented in the central. Indeed, checking the later visual processing marked by stimulus-induced alpha, the eccentricity of 1.3° and "no distractor" manipulation showed a strongly reduced modulation of alpha power during natural walking and the greatest difference to the standing manipulation. This indicated that during natural walking, the visual input in the fovea area was less processed than in peripheral areas. However, my data did not provide conclusive evidence to confirm that, during natural walking, peripheral distractors exerted a stronger influence on behaviour than peripheral targets. Nevertheless, the pattern of d' and the interaction based on stimulus-induced alpha power in my study 3 was consistent with the finding of enhanced peripheral processing.

I further investigated whether enhanced peripheral processing can be replicated in the auditory domain. To this end, I manipulated the location of the burst tone which can induce an ASSR amplitude perturbation. As predicted, the ASSR amplitude perturbation was more strongly modulated during natural walking only when the burst tone appeared in the peripheral location, providing evidence of enhanced auditory peripheral processing. Previously, the significance of peripheral vision in body movement, such as walking, has been well-acknowledged (Vater & Strasburger, 2021; Vater, Wolfe, & Rosenholtz, 2022). The

peripheral visual input is crucial for interpreting the visual flow field to know the speed and direction of locomotion (Banton, Stefanucci, Durgin, Fass, & Proffitt, 2005; Turano, Yu, Hao, & Hicks, 2005). My findings in the auditory domain suggested that the importance of increased peripheral processing extended beyond vision. During natural walking, individuals are exposed to a dynamic and changing environment, with stimuli appearing from various spatial locations. This increased spatial complexity requires heightened sensory processing to detect and analyse relevant information from the peripheral visual field and auditory space (Marigold & Patla, 2008). It might be an across-modality enhancement as a whole during natural walking that contributes to the perception of object movement in the surrounding environment (Rogers, Rushton, & Warren, 2017). The findings in the auditory domain again supported that natural walking influences cognition at a rather general level. Unfortunately, I did not ask participants to perform any specific behavioural task in the auditory experiments, therefore was unable to measure whether there was a corresponding improvement in final behavioural outcomes as previously reported in a visual task (Benjamin et al., 2018; Cao & Händel, 2019). Nevertheless, my auditory experiments provided the first neural evidence showing a spatially specific enhancement of sensory processing due to natural walking in the auditory domain. Interestingly, when calculating a neural marker indexing a spatial processing preference (stronger entrainment or processing side), I showed that the stronger entrainment or processing side was modulated by the walking path, in other words, dependent on the locomotion route (study 4). This dependence on the locomotion route will be discussed in 7.4. Overall, enhanced spatially specific modulation in both vision and audition and the dependence on the locomotion route reinforces the assumption that natural walking affects information processing in a rather general way.

Spatially specific modulation seems to be distinct from the feature-independent modulation due to walking. First, those two effects were observed based on different neural markers. In the visual study, the modulation of the early ERP amplitude due to natural walking was not dependent on the eccentricity as indicated by stimulus-induced alpha power (Chen et al., 2022a, 2022b). Also, the ASSR amplitude perturbation did not show a general increase or decrease during natural walking independent of burst tone location as the ASSR power showed. Second, unlike the general sensory processing which was robustly linked to alpha oscillation, the spatially specific modulation due to natural walking showed a more complex

relationship to alpha oscillation. In my studies, the spatially specific modulation due to natural walking observed with post-stimulus alpha power was not correlated with the pre-stimulus ongoing occipital alpha oscillation modulation (Chen et al., 2022b). In the auditory study, the modulation of burst tone-induced ASSR amplitude perturbation showed no correlation with ongoing alpha power modulation. However, there existed evidence indicating that increased processing of peripheral visual input due to natural walking was associated with altered inhibitory processes during natural walking. This can be supported by the positive correlation between ongoing alpha oscillations and the changes in SSVEP amplitude (Cao & Händel, 2019). Additionally, in my study 4, the ASSR power, and the ASSR lateralisation which were linked to modulation of occipital alpha oscillation, indeed reflect the processing specifically of the peripheral input. This was because the auditory stimuli were delivered to the left and right ears, thereby establishing a peripheral stimulus condition. I can only speculate that whether or not it was linked to alpha oscillation might be based on different tasks, the different neural makers induced by specific stimuli of the spatially specific effect. Even the ongoing alpha, whether it was pre-stimulus or ongoing with stimulus all mattered. Further investigations are needed to investigate the complex relationship between modulations of occipital alpha oscillation and the spatially specific processing due to natural walking.

Overall, my research showed that natural walking induced an internal state change that affects various cognitive processes beyond vision. The internal state change predicted an enhancement in temporally early visual processes and primary auditory brain activity. This can be interpreted as a general effect on early sensory processes. Besides, my research provided additional support for the existence of a secondary, distinct process modulation induced by natural walking. This second process was specific to peripheral sensory input and was affected by natural walking within both the visual and auditory domains. Nonetheless, a potential limitation to consider is the lack of additional evidence demonstrating the correlation between the modulations of various cognitive processes in both vision and audition. This correlation would provide stronger evidence indicating the modulation of natural walking indeed reflect a change in general internal state. It would be valuable to carry out experiments that simultaneously investigate both visual and auditory processing using the same participants in a consistent setup across modalities.

7.3.3 Influence on higher cognitive processes such as creative thinking

Does the change of internal state due to natural walking also have an impact on higher cognitive processes? Previous studies have reported that walking led to improved divergent thinking performance compared to a stationary state (Andolfi, Nuzzo, & Antonietti, 2017; Kuo & Yeh, 2016; Leung et al., 2012; Oppezzo & Schwartz, 2014; Zhou, Zhang, Hommel, & Zhang, 2017). However, whether these cognitive processes' modulation due to body movement was indeed related to an internal state change has not been established. In my study 5, I, therefore, examined the ongoing occipital alpha power and behavioural performance in a divergent thinking task while participants engaged in different movement states. In addition, I manipulated the factor of movement restrictions, based on the previous studies that underscored the importance of an unrestrictive body state in facilitating divergent thinking (Andolfi et al., 2017; Kuo & Yeh, 2016; Leung et al., 2012; Murali & Händel, 2022). The results showed a reduction in occipital ongoing alpha power during natural walking compared to sitting, as well as during unrestricted conditions compared to restricted conditions. Importantly, I confirmed a correlation between modulation of occipital ongoing alpha power and change in behavioural performance. The decreased occipital alpha power was observed during both the time when the creative task was being actively solved (think time) and during baseline periods unrelated to the task. The reduced ongoing alpha power during natural walking compared to standing suggested a body state effect that is independent of the specific task being performed. This effect was consistent with the reduction being consistently observed irrespective of lighting conditions (Cao et al., 2020) and regardless of whether visual (Chen et al., 2022a, 2022b) or auditory tasks were involved (study 4).

Interestingly, not only body movement but also the movement restriction, i.e. am I allowed to freely executing movements, affected occipital alpha power and creative ideation. This might have several reasons. One potential explanation is that already the possibility to freely move can change the state and accordingly reduce alpha power. This emphasizes not only a physical free state but also a mental one. Leung et al. (2012) showed that participants who walked freely showed better divergent thinking performance than participants who walked along a rectangular path around the square box. Similarly, a study measured the divergent thinking performance in three movement conditions: free-walking, walking in a pre-defined path, and walking in a less predictable path generated by another person walking

freely (Kuo & Yeh, 2016). This study showed that the free-walking group performed better than walking in a pre-defined path, and walking according in a path generated by another person who is walking freely. Their findings again suggested the importance of mentally free walking. Another possibility is that also smaller movements were reduced during the restricted state. This might include head- and eye movements, but could also include other small movements by changing the dynamic of the executed movement. The influence of natural walking on cognition might also rely on those small body movements to work in a general way. Therefore, a changed movement output during phases without restriction might introduce the alpha power modulation.

But how can reduced occipital alpha power, which I suggested to be related to decreased inhibition, be beneficial for creative thinking? Can creative ideation be influenced by increased processing of the task-related stimulus? In my case, increased early processing of the auditory presentation of a single word is unlikely to change how divergent the ideas are that can be associated with this word. I therefore interpret the positive effect of natural walking on divergent thinking via an attentional state change. This will be discussed below (6.4).

It is worth noting that my study is not the first to report a link between alpha power and creativity. Prior research has indicated that higher creativity was positively linked to alpha power, albeit mainly at frontal electrode sites (Fink, Grabner, Benedek, & Neubauer, 2006; Fink, Schwab, & Papousek, 2011; Gonen-Yaacovi et al., 2013; Kraus, Cadle, & Simon-Dack, 2019; Lustenberger, Boyle, Foulser, Mellin, & Frohlich, 2015). For example, the divergent training group displayed higher task-related synchronization of frontal alpha activity than the control group (Fink, Grabner, Benedek, & Neubauer, 2006). In a review by Fink and Benedek (2014), they summarized that such alpha power increase reflects creativity-related task demands (Fink, Benedek, Grabner, Staudt, & Neubauer, 2007; Jauk, Benedek, & Neubauer, 2012; Krug, Molle, Dodt, Fehm, & Born, 2003) and the originality of ideas. Accordingly, it is important to differentiate the site of alpha prevalence.

Considering the site of alpha prevalence, some studies have revealed a link between enhanced posterior parietal right hemisphere alpha power and creativity. Fink, Grabner, et al. (2009) have shown that individuals displaying higher levels of originality exhibited a

pronounced hemispheric asymmetry in alpha activity, with stronger task-related alpha synchronization in the right hemisphere compared to the left hemisphere. This right-hemispheric increase associated with creativity has been consistently supported by subsequent studies with normal people and also for dancers or musicians (Benedek, Bergner, Konen, Fink, & Neubauer, 2011; Berkowitz & Ansari, 2010; Fink, Graif, & Neubauer, 2009; Schwab, Benedek, Papousek, Weiss, & Fink, 2014). In study 5, I also observed a similar right alpha lateralisation that was linked to the divergent thinking score. Considering the effect of body movement and movement restriction, I found that stronger right-hemisphere alpha lateralisation during think time was more pronounced during an unrestricted body state compared to a restricted body state. Importantly, the alpha lateralisation (at least during sitting) was not a state effect but specific to the time when ideas needed to be created (think time). This finding was consistent with previous research indicating that an increase in right posterior hemispheric alpha power is linked to creativity, particularly during the idea-generation phase. I tested if the alpha lateralisation was connected to the described relative alpha power effect. While I did find the effects to be partly overlapping in electrodes, no indication that alpha power correlated with alpha lateralisation strength was found. This could potentially indicate distinct effects of bodily state on different facets of cognitive processing, a phenomenon that is also applicable to higher-order cognitive processes like divergent thinking.

Overall, the changed internal state during natural walking also influences higher cognitive processing which is not related to the modulation of basic sensory processing. A higher level influence of natural walking on cognition must therefore be assumed, this will be discussed in the next section (7.4).

7.4 Is attention the underlying mechanism of how walking influences cognition?

Do the findings described above fit to general concepts in psychology, such as attention? Attention is a fundamental process that exerts influence over various cognitive processes and behavioural outcomes. Throughout my studies, attention could be considered as an underlying mechanism through which natural walking affects both basic sensory processing and higher cognitive functions such as divergent thinking. Specifically, my studies suggested that natural walking could change attention in two ways: i) natural walking shifts

the focus of attention towards peripheral input for audition and vision, leading to a spatially specific increase in sensory processing and affecting other cognitive processes like creativity. ii) natural walking reduces inhibition which affects early visual and auditory processing in a general way, and this reduced inhibition might be equivalent to an increased attentional state. However, the attentional state change does not necessarily lead to a change in detection or discrimination related behavioural performance.

Natural walking shifts the focus of attention toward peripheral input

That more attention is shifted to the periphery could be one mechanism through which walking leads to enhanced peripheral processing. In Cao and Händel (2019)'s study, pre-target-induced SSVEP was more strongly modulated by the surrounding contrast during natural walking compared to standing. They found a positive correlation between ongoing alpha oscillations and the changes in SSVEP amplitude. As alpha power over the occipital cortex can indicate the extent of the attentional focus (van Dijk, Schoffelen, Oostenveld, & Jensen, 2008), a reduced occipital alpha power could show a reduced focus of attention on the fovea, where the behavioural task was presented. Their behavioural results showed that the difference between standing and walking was reduced when the target appeared in the peripheral compared to the central area. It indicated an improved processing of peripheral input during natural walking compared to standing. This behavioural finding provided support for the assumption of a modulation of attention, e.g., enhanced attention to the peripheral input. Similarly, in my visual study using a discrimination task (Chen et al., 2022b), for no distractor condition, the d' difference between standing and walking was larger for centre and smallest for a peripheral location with an eccentricity of 9°. This could indicate improved visual processing during natural walking when the stimulus was in a peripheral location, which was also likely to be a result of possibly the shifted focus of attention. In my auditory experiment (study 4), I manipulated the burst tone to appear either in a central or peripheral location. Importantly, the burst tone can be viewed as attention-grabbing input. The result showed that the ASSR amplitude perturbation induced by the burst tone was more strongly modulated during natural walking only when the burst tone appeared in the peripheral location. Earlier work showed a perturbation of the ongoing ASSR amplitude was when subjects responded to simultaneous oddball task (using discreet tone stimuli), indicating a

shift of attention to the upcoming stimulus (Rockstroh et al., 1996). The perturbed ASSR amplitude can also be induced by distracting stimuli and was argued to serve to momentarily decrease attention to the steady-state stimuli (Ross, Herdman, & Pantev, 2005b). My results of a strongly reduced ASSR amplitude during natural walking, induced by a peripheral burst tone, therefore could be interpreted as participants allocating more attention towards the periphery during natural walking. These auditory findings suggested that the phenomenon of attentional shift is not exclusive to the realm of vision but extends to audition as well.

Natural walking possibly shifts the focus of attention towards peripheral input for audition and vision. Such broadened attention could lead to a spatially specific increase in sensory processing. Would the broadened attention during natural walking also function as a mechanism through which walking influences higher-level internal cognitive processes, such as divergent thinking? Indeed, in study 5, an increased processing of the auditory presentation of a single word was unlikely to change how divergent the ideas are that can be associated with this word. The influence of natural walking on higher-level cognition is therefore more likely to be associated with a higher-level mechanism. One view that has been raised before was that the depletion of cognitive resources facilitates divergent thinking (Radel, Davranche, Fournier, & Dietrich, 2015). Zhou et al. (2017) argued this could explain why they found a worse performance during lying and sitting compared to standing while keeping balance since standing up and keeping balance was the most depleting condition and exhausted the most control resources. However in my study 5, one might expect more cognitive resources to be used if they follow the many instructions for the restricted condition, an therefore expect a better performance. However, the behavioural data showed decreased performance in the restricted condition compared to unrestricted states. Accordingly, this did not comply with the cognitive resources explanation. This finding suggested that improvement is unlikely based on the amount of cognitive or attentional resources. Murali and Händel (2022) have discussed this change of attentional focus as the mechanism of why the unrestricted state leads to improved divergent thinking compared to the restricted state, but no neural evidence was provided.

We could see an intriguing behavioural finding that lent support to the notion that the distribution of attention affects creativity. For example, it was found that creative individuals

tend to have a broader attentional focus than less creative individuals (Dykes & McGhie, 1976; Martindale, 1999; Mendelsohn & Griswold, 1964, 1966). Attention broadening training can also enhance creative performance (Memmert, 2007).Friedman, Fishbach, Förster, and Werth (2003) manipulated the attentional distribution by asking participants to first complete visual tasks that forced them to focus attention on a comparatively broad or narrow visual area. They showed that broad, compared to narrow initial focusing of attention led to a better performance in a following task which included a divergent thinking process. The improvement can be observed when participants were attending to bigger stimuli, a way again could be considered as a manipulation of attentional focus (Nijstad, De Dreu, Rietzschel, & Baas, 2010).

In electrophysiology, attention-related modulation can be marked by the change in occipital alpha power (van Dijk et al., 2008), and alpha power modulated by walking seems related to the broadening of the focus of attention (Cao & Händel, 2019). If the broadened attentional distribution is the mechanism that led to the improved divergent thinking due to natural walking, we should expect a corresponding reduced occipital alpha power during natural walking compared to standing which predicts better divergent thinking performance. My results supported this prediction, showing the correlation between improved creativity and decreased occipital alpha power during walking. Accordingly, we can also assume that the unrestricted state leading to better divergent thinking might share the same underlying mechanism as the change induced by walking, as they are all change in body state. I interpret that an unrestricted state also leads to an broadened attentional state marked by reduced occipital alpha power. In addition, studies have shown that during sitting, posture can make a difference in creativity (Andolfi et al., 2017; Michinov & Michinov, 2022). Specifically, sitting in an open posture leads to better divergent thinking than closed posture. The authors interpreted the modulation by posture as a reflection of a change in mental framework, however without clear evidence to support this assertion. Based on my findings, another plausible explanation could be sitting with an open posture leads to a more widespread distribution of attention. Nevertheless, to gain a more comprehensive understanding, more thorough investigations could include additional strategies to manipulate attention distribution while recording neural signals like alpha power.

The general attentional state during natural walking

As shown in the previous section (section 7.2 and 7.3), I found a decreased occipital alpha power due to natural walking which was independent of the change in visual and auditory input. The reduction predicted enhanced temporally early visual processes and primary auditory brain activity and might reflect a reduced inhibition. Could these enhanced early sensory processes also be associated with a change in attention, similar to the presumed shift of attention towards the periphery during natural walking? Building upon the outcomes of my investigations with visual tasks, I argue that this reduction in occipital alpha power can be seen as a general attentional state change, without necessarily lead to a change in detection or discrimination related behavioural performance.

Studies in mice proposed that attention- and running-dependent modulation of neural responses might engage similar mechanisms, such that neurons modulated by attention may also be more likely to be modulated by the active behavioural state (Dadarlat and Stryker, 2017; Mineault et al., 2016). However, contrary to this, Kanamori and Mrsic-Flogel (2022) specifically tested how visual responses of V1 neurons were modulated by global changes in behavioural state and attentional state, and they found no correlation between the strength of modulation by spatial attention and by body movement (running). These results suggested that attentional mechanisms did not necessarily underlie changes in neural markers of early sensory processes that are modulated by natural walking.

In human studies, an attentional effect is usually associated with a change in objective performance such as detection or discrimination rate. In my auditory studies, I cannot investigate whether the sensory processing of auditory input is associated with behavioural change since I did not include a behavioural task. However, in the visual experiment, I did not find a behavioural association between objective discrimination performance and the modulation of neural markers of early sensory processes. Specifically, the pre-stimulus occipital alpha power was found to be correlated with reaction time, but not with d' (a measure of discriminability). This suggested that the attentional state might only influence certain aspects of behavioural outcomes, such as the speed of the general sensory processing. Some previous studies have suggested an exclusive link between pre-stimulus alpha power and subjective measures such as subjective visual awareness (Benwell, Coldea, Harvey, &

Thut, 2022; Benwell, Keitel, Harvey, Gross, & Thut, 2018; Benwell et al., 2017; Britz, Diaz Hernandez, Ro, & Michel, 2014). Specifically, higher pre-stimulus power predicted lower visual awareness ratings, a measure of perceived stimulus visibility, but not discrimination accuracy (Benwell et al., 2022). In addition, studies using location detection or change detection tasks found that the score of subjective awareness enhancement was associated with an early negative posterior component around 180–280 ms (VAN, visual awareness negativity). This VAN component has a similar feature to the N1 component in my visual study (Koivisto & Grassini, 2016; Koivisto & Revonsuo, 2003). Following those findings, in my study, a lower alpha power due to natural walking could mark an enhanced awareness. An increased awareness, in my case due to natural walking, may only facilitate the processes indexed by reaction time, while not necessarily leading to an improvement in every aspect of performance. This could lead to cases where the detection or discrimination performance is reduced during walking but the reaction time, improved due to awareness, shown no walking induced reduction. This elucidates that some studies, while reporting lower accuracy or detection rates due to body movement compared to a stationary state, did not uncover a statistically significant decline in reaction time performance (Bradford, Lukos, Passaro, Ries, & Ferris, 2019; Chen et al., 2022b; De Sanctis, Butler, Malcolm, & Foxe, 2014).

To be noted, awareness and attention have been discussed as intricately intertwined in cognitive psychology (Koivisto & Revonsuo, 2010; Lamme, 2003), therefore a change in awareness could also be associated with or without attention change. However, this is not a topic of interest in the current project. There could also be alternative explanations for the exclusive connection between pre-stimulus alpha activity and reaction time, for example the stimulus processing efficiency associated with short-term visual memory encoding (Nenert, Viswanathan, Dubuc, & Visscher, 2012). In my project's context, by proposing the term 'attentional state', I refer to a natural walking-induced change in perceiving and processing the general input which was not spatially specific. What's important is that this attentional state change does not necessarily result in alterations in detection or discrimination-related behavioural performance.

Attention is modulated by a natural walking path

In the auditory study, I found that the processing of ongoing peripheral auditory input was modulated by the walking path. Specifically, I calculated an ASSR lateralisation index by comparing the responses to different tones presented on the left and right side (left 39Hz and right 41Hz). This index can reflect which side received stronger processing. By comparing the ASSR modulation index between left turns and right turns, a distinct ASSR modulation index pattern was observed during the walking path. The pattern showed that the stronger entrainment power was always in line with the turning direction, i.e. for a left turn, the stronger entrainment direction always pointed to the left side; for a right turn, the stronger entrainment direction always pointed to the right side. This also meant that the ASSR lateralisation index had to change with respect to the participant's view: the stronger entrainment side before the 0 time point was directed inward (aligned with the turn direction and to the left side of the participant); when the participant walked towards the turn direction (i.e. around the 0 time point), the entrainment was more balanced between left and right, suggesting a forward orientation with respect to the participant; after the 0 time point, the entrainment was directed outward (opposite to the turn direction and the participant's right side).

The ASSR lateralisation index changed with respect to the participant's view in an inward-forward and outward pattern. This pattern seemed to align well with the concept of active sensing, an active approach to gather data from the environment through movements for an optimized perception (for reviews, see Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010; Yang, Wolpert, & Lengyel, 2018). According to an active sensing view, one does not simply stare at a fixed spot and passively wait for events to unfold, instead, one actively samples the scene through a systematic pattern of eye movements and fixations in vision (Martinez-Conde et al., 2008) and through head orientations in audition (Risoud et al., 2018). This could nicely explain why I did not observe always left-ward or right-ward lateralisation dependent on turning left or turning right from a participant's view. The active sensing framework proposes that the motor system can influence perception by directly generating sensory input through the execution of motor actions. For instance, actions like ocular saccades trigger specific visual stimulation, while sniffs generate airflow and affect odour perception (Scott-Johnson, Blakley, & Scott, 2000). This process shapes the specific content of sensory information flowing from the bottom up (Morillon, Hackett, Kajikawa, &

Schroeder, 2015). However, in current experiments, the auditory input was played via a pair of inserted earphones, and the volume was adjusted to a level where it surpassed the threshold for perceiving external auditory inputs. Such an experimental set-up ensured that the auditory input participants heard remained unchanged regardless of the body movement. In this case, a processing change dependent on the walking path but observed without a change in actual auditory input would indicate an additional top-down effect due to active sensing.

What might be the such top-down control? Previous studies, which examined changes in dichotic ASSR signals in response to left- and right-sided stimuli, have demonstrated a change in ASSR amplitude due to attention. Specifically, more attention to a particular side leads to enhanced ASSR amplitude in the corresponding side (Bharadwaj, Lee, & Shinn-Cunningham, 2014; Manting, Andersen, Gulyas, Ullen, & Lundqvist, 2020; Ross, Picton, Herdman, & Pantev, 2004; Skosnik, Krishnan, & O'Donnell, 2007; Voicikas, Niciute, Ruksenas, & Griskova-Bulanova, 2016). The changed ASSR lateralisation dependent on the walking path may reflect a change of attention between left and right while turning. Our findings suggest that the changes in attention alongside the walking path are also an important part of a strategy of active sensing. During turning, not only the motor output, e.g. the body movement and associated body sensor is adapted to the walking path, but also the attention might be adapted. Participants may change the focus of attention in the given walking path to better process the sensory input to optimize navigation during natural walking. The top-down attentional mechanism enforced the oscillatory entrainment to the continuous auditory input dependent on the walking path (Schroeder & Lakatos, 2009). Since the walking path was pre-defined and provided a clear indication of the direction to follow, participants could mentally encode this simple "map-like" information. By encoding the spatial layout of the pathway in their minds, they first had a global clear direction, e.g. a generally left turn or right turn. At the same time, the changing inward-forward-outward ASSR lateralisation pattern from the participants' view suggested another interesting process that might occurred during turning: participants seemed to effectively anticipate upcoming turns and adjusted their attention accordingly in an active sensing manner. Overall, the finding that the strength of sensory entrainment was modulated by the walking direction, marked by ASSR lateralisation change suggested that attention might be part of active sensing during natural walking.

In general, attention can be considered a likely mechanism through which natural walking influences both basic sensory processing and higher cognitive functions, such as divergent thinking. Natural walking could lead to a shift of the focus of attention towards peripheral input for audition and vision, this broadened attention could also affect other cognitive processes like creativity. In addition, the processing of peripheral input can be modulated based on the walking path might also be driven by changes in attention allocation. Also, that natural walking affects temporally early visual processes and primary auditory brain activity could be based on an increased attentional state, or an awareness change. However, it's crucial to acknowledge another significant shortcoming of my research, namely that I did not directly manipulate attention. Furthermore, the interpretation of awareness was not derived from an experimental manipulation but rather relied on previous studies. Further experiments are needed to confirm whether the observed natural walking-induced reduction in alpha power, the changes in early sensory processes (marked by early ERPs and signals in primary cortical areas) and behavioural measures of creativity scale with more specific attention-related manipulations.

7.5 General conclusion:

The findings of this project showed that natural walking reduces occipital ongoing alpha activity independent of walking induced changes in visual and auditory input. This effect is introduced by the movement itself. There is indication that particularly natural body movement, e.g. natural walking, reveals a full-size effect. That the reduction of alpha power, although centred in the occipital cortex, modulates various cognitive processes beyond vision, suggests a general change in the internal state.

The modulation of cognitive processes included a general enhancement in temporally early visual processes and primary auditory brain activity. They could be predicted by the walking-induced change in ongoing occipital alpha oscillation. I argue that the enhancement in such early sensory processes due to natural walking is based on disinhibition reflected by the reduced occipital alpha power.

In a separate process, natural walking specifically enhanced the processing of peripheral sensory input in the auditory domain, following previous visual findings. This

spatially specific change was additionally modulated by the walking path and interpreted to be achieved through a change in the spatial focus of attention. The broadened focus of attention might also serve as mechanism underlying the enhanced divergent thinking performance during natural walking, which I found to be correlated with the walking induced occipital alpha power reduction.

Overall, my thesis provides ample evidence that natural walking modulates the internal state which leads to a change in basic and higher cognitive processes with respect to stationarity.

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9. Appendix

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C. Affidavit

Affidavit

I hereby confirm that my thesis entitled *How natural walking changes occipital alpha oscillations and concurrently modulates cognitive processes* is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore, I confirm that this thesis has not yet been submitted as part of another examination process neither in identical nor in similar form.

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Figure	**Author Initials,** Responsibility decreasing from left to right				
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4	XC	LC	BH		
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3	XC	LC	BH		
4	XC	LC	BH		
5	XC	LC	BH		
6	XC	LC	BH		

Table	**Author Initials,** Responsibility decreasing from left to right				
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Manuscript 4 (complete reference): Chen, X., Cao, L., Wieske, R.E., Gramann, K., & Händel, B.F. (in preparation). Walking modulates active auditory sensing.

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3	XC	BH	LC	KG	RW
4	XC	BH	LC	KG	RW
5	XC	BH	LC	KG	RW
6	XC	BH	LC	KG	RW
7	XC	BH	LC	KG	RW
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I also confirm my primary supervisor's acceptance.

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Study Design Methods Development	LC, BH	XC			
Data Collection	LC	XC	BH		
Data Analysis and Interpretation	LC	BH	XC		
Manuscript Writing Writing of Introduction Writing of Materials & Methods Writing of Discussion Writing of First Draft	LC,BH	XC			

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Study Design Methods Development	XC	LC	BH		
Data Collection	XC	LC	BH		
Data Analysis and Interpretation	XC, LC	LC	BH		
Manuscript Writing Writing of Introduction Writing of Materials & Methods Writing of Discussion Writing of First Draft	XC	LC, BH			

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Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	XC	LC	BH		
Data Collection	XC	LC	BH		
Data Analysis and Interpretation	XC	LC	BH		
Manuscript Writing Writing of Introduction					

Writing of Materials & Methods Writing of Discussion Writing of First Draft	XC	LC, BH			

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Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	BH	XC, LC	KG	RW	
Data Collection	XC	LC	BH	KG	RW
Data Analysis and Interpretation	XC	BH	LC	KG	RW
Manuscript Writing Writing of Introduction Writing of Materials & Methods Writing of Discussion Writing of First Draft	XC, BH	LC	KG	RW	

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Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	BH, SM	XC			
Data Collection	SM	XC	BH		
Data Analysis and Interpretation	XC	BH, SM			
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