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Abstract: Walking provides the motor foundation for navigation, while navigation ensures that walking is purposeful and adaptive to environmental contexts. Sensory processing of environmental information acts as the informational bridge that connects walking and adaptive navigation. In the current study, we assessed if walking and the walking direction influences neuronal dynamics underlying environmental information processing. To this end, we conducted two experiments with 12 male and 18 female participants while they walked along an 8-shaped path. Auditory entrainment stimuli were continuously presented, and mobile EEG (electroencephalogram) was recorded. We found increased auditory entrainment (auditory steady-state response) and early auditory evoked responses during walking compared to standing or stepping-in-place. We also replicated the well-established reduction of occipital alpha power during walking. The increase of auditory entrainment and the decrease of alpha power were correlated across participants. In the second experiment, randomly presented transient burst tones led to a perturbation of the auditory entrainment response. The perturbation response was stronger during walking compared to standing, however, only when the burst tones were presented to one ear but not to both ears. Most importantly, we found that the auditory entrainment was systematically modulated dependent on the walking path. The entrainment responses changed as a function of the turning direction. In general, the current work shows that walking changes auditory processing in a walking path-dependent way which might serve to optimize navigation. The walking path related modulation might further reflect a shift of attention, marking a form of higher-order active sensing.

Significance Statement: In this mobile EEG walking study, we uncovered a dynamic shift in auditory attention that aligns with changes in walking trajectory. Specifically, during turns, the brain prioritizes auditory input from the side of turn direction before the turn apex, then shifts preference to the opposite side. These findings reveal an active sensing mechanism that goes beyond simple motor adjustments to adjust sensory input but suggests that the brain dynamically optimizes the processing of sensory input e.g. to facilitate navigation. This study offers potential applications for understanding spatial awareness in real-world environments and improving navigational aids.

Introduction

The ability to move is an essential feature of living organisms. With the development of mobile electroencephalogram (EEG), growing evidence in human studies points to a close relation between body movements and cognition (Borghi & Cimatti, 2010; Koziol, Budding, & Chidekel, 2012; Schmidt-Kassow & Kaiser, 2023; Stangl, Maoz, & Suthana, 2023). For example, walking has been shown to influence a wide range of cognitive processes, from basic sensory processing (Bullock, Cecotti, & Giesbrecht, 2015; Cortney Bradford, Lukos, Passaro, Ries, & Ferris, 2019; Davidson, Verstraten, & Alais, 2024; Yagi, Coburn, Estes, & Arruda, 1999) to higher order processes like learning and creativity (Frith, Ryu, Kang, & Loprinzi, 2019; Händel, Chen, & Murali, 2024; Lhuillier, Gyselinck, Piolino, & Nicolas, 2021; Wilson & Gibbs, 2007).

In electrophysiology, a robust finding in actively moving humans is the reduction of ongoing alpha power in the parieto-occipital cortex, which has been shown to be independent of electrode impedance, eye movements, and visual input (Cao, Chen, & Händel, 2020; Ehinger et al., 2014; Kuziek, Redman, Splinter, & Mathewson, 2018; Lin, Wang, Wei, & Jung, 2014; Robles et al., 2021; Scanlon, Townsend, Cormier, Kuziek, & Mathewson, 2019; Shaw et al., 2018; Wagner et al., 2019; Zink, Hunyadi, Huffel, & Vos, 2016). Alpha activity has been associated with neural inhibition (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007). Consistent with this, stronger event related potentials (ERP) during body movements in the visual (Bullock et al., 2015; Chen, Cao, & Haendel, 2022a, 2022b; Dodwell, Liesefeld, Conci, Muller, & Tollner, 2021) and auditory (Scanlon et al., 2019; Vaughn et al., 2021) domains have been reported, which likely resulted from a disinhibition process due to alpha reduction (Chen et al., 2022a).

Similarly, animal studies also showed that the firing rates of neurons in the primary visual cortex are modulated by the running speed and that this modulation persists in complete darkness (Ayaz, Saleem, Scholvinck, & Carandini, 2013; Dipoppa et al., 2018; Kanamori & Mrsic-Flogel, 2022; Neske, Nestvogel, Steffan, & McCormick, 2019; Niell & Stryker, 2010).

Locomotion can lead to a spatially specific change in sensory processing. Cao and Händel (2019) found that surrounding contrast impaired the detection of central targets during walking. This was accompanied by reduced occipital alpha power, suggesting less inhibition and enhanced visual processing for peripheral input (see also Benjamin, Wailes-Newson, Ma-Wyatt, Baker, and Wade (2018)). Using a single-stimulus visual detection paradigm, Reiser, Arnau, Rinkenauer, and Wascher (2022) observed that posterior lateralized ERP latencies were shorter during walking than during stationary periods, but only for stimuli presented in extrafoveal (peripheral) locations. These findings point to a redistribution of visual attention during natural movement as an optimization strategy for processing task-relevant input, which was supported by studies on head and eye movements while walking (Imai, Moore, Raphan, & Cohen, 2001; Tuhkanen, Pekkanen, Wilkie, & Lappi, 2021).

In the present study, we were interested in the effect of walking on auditory processing. It has been shown that walking involves cross-model activations (Brungart, Kruger, Kwiatkowski, Heil, & Cohen, 2019). Comparable brain responses to environmental boundaries in both auditory and visual maze navigation tasks have also been reported (Miyakoshi, Gehrke, Gramann, Makeig, and Iversen (2021). Therefore, like in the visual domain, walking may influence auditory processing. In two experiments

combining mobile EEG recording and a well-defined walking task, we showed an enhanced auditory entrainment (using the auditory steady-state response, ASSR) during walking compared to standing and stepping in place, which was robustly predicted by a decreased occipital alpha power during walking. Furthermore, we found that dichotic, but not diotic, tones led to an enhancement of ASSR perturbation during walking, which indicates a prioritised processing of auditory input with a peripheral origin in the environment. Importantly, when participants made turns during walking, dynamic changes in the auditory entrainment introduced by the input from the side of the turning direction were observed, indicating a change of auditory attention in accordance with the walking trajectory.

Methods

Participants

35 participants recruited from a local participants pool via the SONA system took part in the study (21 females, mean age = 28.05 years, SD = 3.51). 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 for this participant. 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).

Experimental design

The study included 2 experiments. The first experiment focused on the ASSR, and the second experiment aimed to also investigate a stimulus induced perturbation of the ASSR power. 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 completed the three conditions with an order of stepping – walking – standing, and the other half of the participants with an order of standing – walking – stepping. In the standing condition, participants were instructed to stand in the centre of the marked walking pathway (Figure ***1a***, green dot). In the stepping condition, participants were asked to walk on the spot in the same location as in the standing condition (Figure ***1a***, green dot). In the walking condition, participants were asked to walk in an "8" shaped pathway (Figure ***1a***, 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 were asked not to strictly fixate at 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 ***1b***, 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 ***1a*** 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 ***1a*** walking path 2. The walking speed was trained before the start of the experiment to ensure that participants took approximately 12 seconds 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 experiment, participants were exposed to a continuous stream of sinusoidal amplitude-modulated tones to elicit an auditory steady-state response (ASSR). The tone in the left ear was modulated at 39 Hz, and 41 Hz in the right ear (Figure ***1b***). We chose these two frequencies as ASSR power was found to reach a maximum response around 40 Hz in humans (Galambos, Makeig, & Talmachoff, 1981; van der Reijden, Mens, & Snik, 2001). The carrier frequency was set to 1000 Hz, with a modulation depth of 100%. The auditory stimuli had a sampling rate of 44100 Hz. Participants were not required to perform any behavioural task in response to the tones.

Experiment 2

Each participant completed four testing blocks, each containing a walking and a standing condition similar to experiment 1. 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 ***1a***) of walking was again balanced among participants to control for potential

external confounding variables. The total testing duration for the walking and standing condition was approximately 8 and 2 minutes in each block, respectively.

Participants were exposed to a continuous stream of sinusoidal tones, which were amplitude-modulated at 39 Hz (left ear) and 41 Hz (right ear) as in experiment 1. To perturb the auditory stimuli, burst tones (white noise) lasting 100 ms were intermittently presented diotically or dichotically at unpredictable latencies and order (Figure ***1b***). For diotic perturbation (central burst), the burst tone was presented to both ears simultaneously, and almost all participants reported hearing a burst tone in the frontal midline when they were asked by the experimenter regarding their perception of the diotic perturbation. For dichotic perturbation (left or right burst), the burst tone was only presented in the left ear or the right ear. Participants in this case reported hearing a burst tone in a left or right peripheral location, respectively. In the standing block, participants experienced 8 bursts at intervals of 3 -7s for each burst type (central, left, or right). In the walking block, participants experienced 32 bursts also every 3-7 s for each burst type (central, left, or right) to ensure that enough trials with bursts could be recorded during turning left and right. As in experiment 1, participants were not instructed to respond to or attend to the tones in any particular way.

Data Acquisition

EEG data were recorded using the Smarting mobile EEG system (mBrainTrain LLC, Serbia) with 24-bits resolution. The EEG system provides 24 channels and used wet electrodes located according to the 10% system (covering frontal central, parietal, temporal and occipital areas) 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. The electrode impedance was kept below 15 kOhm.

Motion data were 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) (Kothe et al., 2024). Stimulus generation and presentation were coded in MATLAB (The Mathworks Inc, R2019b) using the Psychtoolbox (Kleiner, Brainard, & Pelli, 2007).

Data analysis

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 ASSR with a clear 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 were first re-referenced to the average of two earlobe electrodes. The data were 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 were then reduced to 16 dimensions using principal component analysis (PCA), followed by independent component analysis (ICA) using the "runica" (Infomax) approach (Delorme & Makeig, 2004). The power spectrum of each ICA component was obtained using Welch's method with a 1 s time window and 50% overlap.

The components with clear ASSR signal at 39 or 41 Hz were selected for further analysis. An example component can be seen in Figure ***2a***. Note that we did not have specific requirements regarding the topographic distribution when selecting the ASSR components. 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' ASSR power from all participants can be seen in Figure ***2b***. In general, the fronto-central area showed the largest ASSR power response. For the selection of the alpha components, the criteria from our previous study were used (Cao et al., 2020). Specifically, four requirements should be met: 1. There should be a local power peak between 6 and 14 Hz in the component's power spectrum; 2. The width of the local peak, which was defined as the

frequency width between the two adjacent local minimums, was required to 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 had to 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) had to be larger than the maximum absolute weight from all other sensors. Following these selection criteria, 8 participants in experiment 1 and 5 participants in experiment 2 were excluded as no components fulfilled the above requirements. On average, with participants who fulfilled the criteria (remaining participants in experiment 1: 22; experiment 2: 23), 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 ***2c***. The topography of the alpha power response for all participants can be seen in Figure ***2d*** for the two experiments. The occipital electrodes showed the strongest alpha power response. Both ASSR and alpha components were subsequently back-projected to the sensor space for further analysis.

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 ***2e***). This corresponds to the middle time point during the turn (Figure ***2f***, 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.

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

For both experiments, the fronto-central electrodes (AFz, Fz, F3, F4, Cz) were included in the ASSR-related analyses, as they covered the main response region where the ASSR power was strongest. 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 components were 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; ASSR frequency; 39 Hz vs. 41 Hz) repeated-measures ANOVA was performed with the parameterized ASSR power. The comparison in experiment 2 focused on the walking and standing conditions. Again, a two-way (movement state: stand vs. walk; ASSR frequency; 39 Hz vs. 41 Hz) repeated-measures ANOVA was performed with the parameterized ASSR power.

279 Furthermore, we examined whether walking led to a decrease in alpha power, as
280 reported in previous studies. The parameterized power was obtained using the same
281 method as for the ASSR power but was based on the identified alpha components. In
282 experiment 1, a one-way (movement state: step vs. stand vs. walk) repeated-measures
283 ANOVA performed with the alpha power ([8 14] Hz) averaged over the two occipital lateral
284 electrodes (O1 and O2). In experiment 2, we compared the average alpha power using
285 paired-sample t-tests between stand and walk. Throughout the results in the manuscript,
286 the alpha power and ASSR power always refer to the parameterized power.

287 ***The ASSR lateralisation analyses***

288 The time resolved ASSR power was obtained through a Hilbert transformation of
289 the band-pass (±0.5 Hz of the frequency of interest) filtered data in each block before
290 epoching data into turning trials. An ASSR lateralisation index was then computed which
291 indexed the lateralisation of entrainment at each time point:

292 ASSR lateralisation index:

$$\frac{\text{39Hz ASSR power} - \text{41Hz ASSR power}}{\text{39Hz ASSR power} + \text{41Hz ASSR power}}$$

293 Since the 39 Hz ASSR tone was consistently presented to the left ear, while the
294 41 Hz tone was consistently presented to the right ear, the ASSR power at 39 Hz would
295 reflect the strength and synchrony of the neural activity in response to left side input, while
296 the ASSR power at 41 Hz would reflect the strength and synchrony of the neural activity

297 in response to right side input. Therefore, a larger ASSR modulation index indicates a
298 relatively stronger processing of the input from left ear while a smaller ASSR modulation
299 index indicates a relatively stronger processing of the input from the right ear.

300 To check whether the ASSR modulation index was influenced by the turning
301 direction, a cluster-based permutation statistical method was used to assess if the ASSR
302 lateralisation index between left turn and right turn was significantly different (Maris &
303 Oostenveld, 2007). The data were shuffled (1,000 permutations) to estimate a 'null'
304 distribution of the t-values based on cluster-level statistics (cluster-defining threshold: $p <$
305 0.05). Significance of the t-value of the original test is assumed if the t-value falls above
306 the upper 5% of permeation t-values. The time window of the statistical comparison was
307 between ([-2 2] s).

308 ***The ASSR perturbation analyses (experiment 2 only)***

309 *The modulation of ASSR perturbation by movement condition*

310 To investigate how the sensory-specific processing was modulated by movement
311 and burst location, we compared the power of the burst tone-evoked ASSR perturbation.
312 A perturbation trial was time locked to the burst tone onset (time 0) and included 2
313 seconds data both before and after the burst tone onset, resulting in a 4-second trial.

314 The burst tone evoked ASSR perturbation was calculated after averaging over all
315 trials in each condition. A baseline correction was performed using a pre-stimulus window
316 ([-400 0] ms) with log transformation. The strength of the ASSR perturbation was
317 calculated as the average power between ([0 700] ms) after the burst tone onset. A 3-

318 way (movement state: stand vs. walk; burst location; left vs. right vs. central; ASSR
319 frequency; 39 Hz vs. 41 Hz) repeated-measures ANOVA was performed with the mean
320 ASSR power perturbation as dependent measure. Throughout the manuscript, we used
321 a Greenhouse-Geisser correction for ANOVA results when necessary, and statistical
322 significance was defined as $p < 0.05$.

323 *The modulation of ASSR perturbation by walking path direction*

324 The onset of the burst tone was further classified based on the direction of turning
325 during which it occurred, i.e. bursts that occurred while turning left and bursts that
326 occurred while turning right. A 3-way (turn direction: left vs. right; perturbation location;
327 left vs. right vs. central; ASSR frequency; 39Hz vs. 41Hz) repeated-measures ANOVA
328 was performed with the mean ASSR power perturbation.

329 ***ERP analyses (experiment 2 only)***

330 To check the auditory evoked response induced by the burst tone, the filtered data
331 were epoched into trials with time window of ± 2 seconds around the burst tone. The EEG
332 data were baseline-corrected by applying a 700 ms pre-stimulus (averaged over ([-700
333 0]) ms) absolute baseline to each trial. The grand average ERP was again based on the
334 fronto-central electrodes (AFz, Fz, F3, F4, Cz). We compared the first and second positive
335 components (named P1 and P2 component henceforth). The time windows of the P1 and
336 P2 components were selected by using a 50 ms window centring the positive peaks of
337 the grand average. In this ERP analysis, a 2-way (movement state: stand vs. walk; burst
338 location: left vs. right vs. central) ANOVA was performed with the P1 and P2 component
339 amplitude separately.

340 ***Correlational analyses***

341 To investigate the potential correlation between the modulation of alpha power due
342 to walking and the neural markers of sensory processing, correlational analyses were
343 performed. Except for the exploratory test for the evoked P2 component, all correlations
344 were one-sided and based on our hypotheses. We utilized the Spearman correlation
345 coefficient for these analyses. Outlier rejection was conducted using the method from the
346 Robust Correlation Toolbox (Pernet, Wilcox, & Rousselet, 2013). Specifically, outliers
347 were identified as the intersection of bivariate flags based on three robust methods: the
348 boxplot method, the median absolute deviation (MAD) method, and the S-outlier method.
349 Only data points flagged by all three approaches were considered outliers

350 Frequency analysis: first, correlation analysis was performed between the alpha
351 power modulation and the ASSR power modulation during walking, averaging between
352 the two frequencies (39 Hz and 41 Hz). This aimed to assess the relationship between
353 alpha power and ASSR power modulation due to walking. Additionally, we examined the
354 relationship between the alpha power modulation and the ASSR power perturbation
355 modulation due to walking, again averaging between the two frequencies (39 and 41 Hz).

356 ERP analysis: Following up on previous studies finding a relationship between
357 alpha power and early evoked responses, we examined the relationship between the
358 modulation of the early burst tone evoked response (P1), and modulation of the alpha
359 power. Additionally, the correlation between the modulations of the P1 component
360 amplitude and ASSR power was also calculated. The relationship between the
361 modulations P2 component and ASSR perturbations was additionally assessed to

362 determine whether the P2 component marks similar processes as those indicated by
363 ASSR perturbations that was modulated by walking.

364 ## Results

365 **Enhanced ASSR power was related to the decreased alpha power during walking**

366 We first compared the overall ASSR power between the three movement states in
367 experiment 1. The two-way (movement state: step vs. stand vs. walk; ASSR frequency;
368 39 Hz vs. 41 Hz) repeated-measures ANOVA was performed with the ASSR power
369 averaged over fronto-central electrodes (AFz, Fz, F3, F4, Cz). The results showed a main
370 effect of movement state ($F(2, 58) = 7.80$, $p = 0.007$), with the ASSR power during walking
371 ($M = 0.32$, $SD = 0.52$) being higher than during stepping ($M = 0.16$, $SD = 0.23$) (post-hoc
372 $t(29) = 2.74$, $p = 0.011$) and during standing ($M = 0.07$, $SD = 0.11$) (post-hoc $t(29) = 2.86$,
373 $p = 0.008$) (Figure ***3a***). The ASSR power during stepping was also higher than during
374 standing (post-hoc $t(29) = 2.49$, $p = 0.019$). The main effect of ASSR frequency was also
375 significant ($F(1, 29) = 5.00$, $p = 0.033$), showing that the power for 39 Hz ASSR ($M = 0.13$,
376 $SD = 0.36$) was higher than the power for 41 Hz ($M = 0.24$, $SD = 0.22$). No other effect
377 was statistically significant.

378 The one-way (movement state: step vs. stand vs. walk) repeated-measures
379 ANOVA performed with the alpha power averaged over the two occipital lateral electrodes
380 (O1 and O2) revealed a significant main effect of movement state ($F(2, 42) = 4.49$, $p =$
381 0.033). The post-hoc t-tests showed that the alpha power was higher during standing than
382 during walking ($t(21) = 2.64$, $p = 0.015$). The alpha power during stepping was also

383 significantly higher than during walking (t(21) = 2.85, p = 0.010). The difference between
384 standing and stepping did not reach significance (t(21) = 1.23, p = 0.232) (Figure ***3b***).

385 To test whether the ASSR power enhancement was associated with the deceased
386 occipital alpha power during walking, a between-participant correlation was performed
387 between the alpha power difference (stand - walk) and ASSR power difference (stand -
388 walk). A significant negative correlation was found (r = -0.44, p = 0.030, one-tailed, Figure
389 ***3c***), showing that lower alpha power was associated with higher ASSR power.

390 We compared again the ASSRs power between the two movement states in
391 experiment 2. The two-way (movement state: stand vs. walk; ASSR frequency; 39 Hz vs.
392 41 Hz) repeated-measures ANOVA was performed with the ASSR power averaged over
393 the fronto-central electrodes (AFz, Fz, F3, F4,Cz). The results showed a main effect of
394 movement (F(1, 27) = 20.67, p < 0.001), with the ASSR power during walking (M = 0.23,
395 SD = 0.31) being higher than during standing (M = 0.08, SD = 0.16) (post-hoc t(27) = -
396 4.55, p < 0.001) (Figure ***3a***). We then performed t-tests comparing the alpha power
397 between standing and walking. The results showed that alpha power was smaller during
398 walking compared to standing (t(24) = 4.53, p < 0.001) (Figure ***4e***). Moreover, the
399 correlation between the modulation of ASSR power and alpha power was also significant
400 (r = -0.53, p = 0.009, one-tailed) (Figure ***4f***).

401 **The strength of ASSR lateralisation is modulated by the walking path**

402 <u>Experiment 1</u>

403 The average ASSR lateralisation index for the left and right turn was computed to
404 reflect the difference in the entrainment response between left and right ears. A larger
405 ASSR lateralisation index indicated more attention to the left ear (or left spatial field). The
406 ASSR lateralisation was time locked to the mid-turn time point, which was the time when
407 participants were at the apices of the 8-shaped walking path. A cluster-based permutation
408 t-test between left turns and right turns revealed a significant difference between the two
409 turn directions during the time window before the mid-turn time point ([-1.20 -0.53]s) (p =
410 0.016) as well as after the mid-turn time point ([0.20 0.99]s) (p = 0.028) (Figure ***4a***). The
411 pattern indicated that spatial auditory processing changed dynamically in accordance with
412 the turning behaviour. Processing was stronger at the side of the turn (e.g. a left turn,
413 increased processing of left spatial input) in the starting phase of turning (before the mid-
414 turn time point at 0 s). However, at the later phase of turning (after the mid-turn). After
415 mid-turn, processing changed to be stronger at the opposite side of the turn (e.g. a left
416 turn, increased processing of right spatial input).

417 Experiment 2

418 Experiment 1 was designed and optimized for the ASSR lateralisation analysis
419 whereas experiment 2 was designed to analyse the processing of a perturbing stimulus,
420 in our case a sound burst. Nevertheless, we tested whether the modulation of ASSR
421 lateralisation by the walking path can be observed in experiment 2 despite the presence
422 of perturbing stimuli. Indeed, the ASSR modulation index showed a similar pattern (Figure
423 ***4c***) as in experiment 1. The cluster-based permutation t-test between left turn and right
424 turn revealed a significant difference between left turn and right turn during the time
425 window before the mid-turn time point ([-1.68 -0.99] s) (*p* = 0.006). However, the

426 difference between left turn and right turn did not reach significance after the mid-turn
427 time point.

428 To rule out potential confounds from muscle-related broad-frequency activity, we
429 tested whether the observed lateralization pattern was specific to the ASSR frequencies.
430 We computed the lateralization index using neighboring frequencies (37 Hz and 44 Hz)
431 and applied the same cluster-based permutation test as in the original analysis. No
432 systematic modulation emerged between left-turn and right-turn conditions for experiment
433 1 and experiment 2 (Text ***S1*** *&* *Figure* ***S1***), and no significant differences in lateralization
434 index were detected. Additionally, the horizontal electrooculogram (HEOG) signal time-
435 locked to the turning events were analysed. There was no consistent or directionally
436 specific drift in the HEOG signal that could account for the observed ASSR modulation in
437 both experiment 1 and experiment 2 (Text ***S2*** *&* *Figure* ***S2***).

438 **Peripheral ASSR power perturbation modulation was enhanced during walking**

439 To test if dichotic sensory input would more strongly affect the ASSR signal during
440 walking, a three-way (movement state: stand vs. walk; burst location: left vs. right vs.
441 central; ASSR frequency: 39 vs. 41) repeated-measures ANOVA was performed. As
442 dependent variable we used the mean amplitude the ASSR perturbation response (39 Hz
443 and 41 Hz, respectively) in the fronto-central electrodes (AFz, Fz, F3, F4, Cz) during ([0
444 700] ms) after the burst tone onset. Results showed a significant interaction between
445 movement state, perturbation location, and ASSR frequency ($F(2, 54) = 3.36$, $p = 0.049$).
446 Further, post-hoc t-tests indicated that when the burst tone appeared in the left ear
447 (perturbing the 39 Hz tone), the 39 Hz ASSR power perturbation was more strongly

448 modulated during walking (M= -1.66, SD = 1.06) compared to standing (M = - 1.23, SD =
449 1.25; t(27) = 2.08, p = 0.047) (Figure ***5a***). When the burst tone appeared in the right ear
450 (perturbing the 41 Hz tone), the 41 Hz ASSR power perturbation was more strongly
451 modulated during walking (M = -1.19, SD = 0.68) compared to standing (M= -0.87, SD =
452 1.05), however the post-hoc t-test was marginally significant (t(27) = 1.92, p =
453 0.065)(Figure ***5b***). When both 39 Hz and 41 Hz tones were interrupted by a burst
454 (perception of a central tone), no significant difference was observed between standing
455 and walking in either 39 Hz (t(27) = 0.22, p = 0.826) or 41 Hz ASSR perturbation response
456 (t(27) = 0.78, p = 0.442) (Figure ***5c***). Additionally, a significant main effect of ASSR
457 frequency was observed (F(1,27) = 14.30, p < 0.001), indicating that the 39 Hz ASSR
458 perturbation response (M = -1.46, SD = 0.93) was stronger than the 41 Hz ASSR
459 perturbation response (M = -0.99, SD = 0.71). No other significant effects were found.

460 We also investigated whether the difference in ASSR perturbation response
461 between standing and walking (average over perturbation locations) could be predicted
462 by the movement related difference in ongoing alpha power. However, the correlation
463 analysis yielded a non-significant result (r = -0.18, p = 0.386), indicating that the
464 modulation of ASSR perturbation during free walking was not associated with the
465 modulation of ongoing alpha activity during walking.

466 **Modulation of peripheral ASSR perturbation was not dependent on the walking**
467 **path**

468 In a next step, we investigated whether the strength of the ASSR perturbation
469 appeared in peripheral location 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 ***6a***, 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 power perturbation between the fronto-central electrodes (AFz, Fz, F3, F4, Cz) within 650 ms after the burst tone onset. In addition to the main effect of ASSR frequency ($F(1, 27) = 8.84$, $p = 0.006$) only the interaction between the perturbation location and the ASSR frequency was significant ($F(2, 54) = 4.51$, $p = 0.017$): the 39 Hz ASSR power was most strongly modulated in the left perturbation condition while the 41 Hz ASSR power 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 ($F(2, 54) = 0.99$, $p = 0.375$) (Figure ***6b***).

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 ***6c***, stronger left entrainment time was marked in blue, stronger right entrainment was marked in red). This 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 within the first 700 ms showed a significant main

493 effect of ASSR frequency (F(1,27) = 6.18, p = 0.019). This suggests that the 39Hz ASSR
494 perturbation amplitude was more strongly modulated compared to 41 Hz ASSR power
495 (Figure ***6d***). No other effects were statistically significant.

496 ## ERP locked to the burst tone onset

497 The ERP was time-locked to burst onset and analysed again at fronto-central
498 electrodes (AFz, Fz, F3, F4, Cz), specifically focusing on the P1 component ([140 190]
499 ms) and the P2 component ([300 350] ms).

500 First, a repeated-measures ANOVA with a two-way design (movement state: stand
501 vs. walk; perturbation location: left vs. right vs. central) was performed, revealing a
502 significant main effect of movement state (F(1, 27) = 4.66, p = 0.04). The P1 amplitude
503 was higher during walking (M = 0.09, SD = 0.70) compared to the standing condition (M
504 = -0.27, SD = 0.09) (Figure ***7a-c***, marked in green). No other effect reached statistical
505 significance. We further investigated the relationship between the P1 amplitude with
506 ongoing alpha oscillations and ASSR power. The modulation of the P1 component
507 amplitude was negatively correlated with the modulation of ongoing alpha power (stand -
508 walk) (r = -0.36, p = 0.049, one-tailed) (Figure ***7d***). This indicated that lower ongoing alpha
509 power was associated with a higher P1 component. Furthermore, the modulation of the
510 P1 component amplitude was positively correlated with the modulation of ASSR power (r
511 = 0.48, p = 0.009, one-tailed) (Figure ***7e***).

512 We also analysed the P2 component ([300 350] ms) using the same two-way
513 repeated-measures ANOVA. We only observed a significant interaction between
514 movement state and perturbation location (F(2, 54) = 4.59, p = 0.017), which indicates

that the P2 component amplitude was smaller during walking when tone was presented dichotically (average between left and right perturbation: $t(27) = 2.70$, $p = 0.012$) but showed no significant difference in the central locations ($t(27) = -0.82$, $p = 0.419$)

Discussion

Enhanced sensory processing during natural walking

In the current study, we found that walking led to 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, Dimitrijevic, & John, 2002; Picton, van Roon, & John, 2009). The cortical sources of the ASSR lie within the primary auditory cortex (Herdman et al., 2003; Ross, Herdman, & Pantev, 2005; Teale et al., 2008). ASSR reduction has been utilized as an indicator of clinical sensory processing dysfunction (Picton, Dimitrijevic, Perez-Abalo, & Van Roon, 2005; Sugiyama et al., 2021). Increased ASSR power during walking 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 cycling (Bullock, Elliott, Serences, & Giesbrecht, 2017).

Notably, the ASSR power during walking was stronger than the ASSR power during stepping in place. Both conditions involve similar motor actions and somatosensory feedback, but only walking includes spatial movement. However, spatial movement independent of motor output appears to be ineffective in enhancing sensory processing (Vaughn et al., 2021). Accordingly, we propose that natural movement, e.g.

motor output that has a certain ecologically valid spatial aim, introduces the strongest changes in sensory processing. Indeed, studies providing evidence for enhanced early sensory processing due to movements, tested natural body movements such as walking (Chen et al., 2022a, 2022b) and outdoor cycling (Malcolm, Foxe, Butler, Molholm, & De Sanctis, 2018; Vaughn et al., 2021). This might also explain some statistically non-significant effects on sensory processing during treadmill walking (Gramann et al., 2010; Malcolm, Foxe, Butler, & De Sanctis, 2015; Nenna, Do, Protzak, & Gramann, 2020).

Additionally, we observed an amplified ERP component following a burst tone (~150 ms after onset) while walking compared to standing. As the auditory P1 component usually has a latency of 50 ms (Hillyard & Anllo-Vento, 1998), we assume that P1 in our case was introduced by the burst tone offset (ASSR tone restart 100 ms after burst onset). An amplification of ERP components during movement is in line with previous studies in both the auditory (Scanlon et al., 2019; Vaughn et al., 2021) and visual (Chen et al., 2022a, 2022b) domain. Overall, the modulation of early auditory ERP components, together with the increased ASSR signal, supports the notion of enhanced processing of auditory input due to active body movements.

Spatially specific processing during walking

We found that dichotic burst tones, i.e. when the burst tone was delivered to only one ear, increased ASSR perturbation during walking. This suggests a walking-induced enhancement of the processing of auditory input that is perceived to appear in a peripheral location. This is in line with previous findings in the visual domain showing that sensory processing particularly in the periphery is affected by body movement in animal

559 (Ayaz et al., 2013) and human research (Benjamin et al., 2018; Cao & Händel, 2019;
560 Reiser et al., 2022). Notably, the increased ASSR perturbation was not merely a side
561 effect of elevated ASSR power during walking, as this would have also led to a walking-
562 induced effect of the central perturbation.

563 Also the ERP analysis showed a spatially specific effect: the P2 component (~200
564 ms after burst tone offset; ~ 300 ms after onset) was smaller during walking than standing
565 for burst tones perceived to appear in the periphery (dichotic). The contrast to the walking
566 induced increase in ASSR perturbation suggests different underlying neural processes.
567 However, the timing of the component does not allow us to conclusively attribute it to the
568 onset, offset, or a blend of both stimulus events. Should it follow the offset by around 200
569 ms, it may correspond to the P2 component which is associated with inhibitory processes
570 (García-Larrea, Lukaszewicz, & Mauguiére, 1992; Senderecka, Grabowska, Gerc,
571 Szewczyk, & Chmylak, 2012; Senderecka, Grabowska, Szewczyk, Gerc, & Chmylak,
572 2012), with stronger inhibition leading to a stronger P2 amplitude (Melara, Rao, & Tong,
573 2002). In line with visual findings (Chen et al., 2022b), the observed walking-related
574 reduction in peripheral P2 may reflect reduced inhibition of peripheral auditory input
575 during walking.

576 Peripheral visual input is essential during walking to interpret motion speed and
577 direction from the visual flow field (Banton, Stefanucci, Durgin, Fass, & Proffitt, 2005;
578 Turano, Yu, Hao, & Hicks, 2005). The here reported auditory findings suggest that the
579 importance of peripheral input processing extends beyond vision. The auditory neural
580 modulation might be part of a cross-modality enhancement that contributes to the

perception of object movement in the surrounding environment (Rogers, Rushton, & Warren, 2017) which could ultimately assist complex processes like navigation.

Enhanced sensory processing related to alpha power

In both experiments, we replicated the well-established reduction in alpha power due to body movements, as reviewed in the introduction. Importantly, we find that the decreased alpha power due to walking was negatively correlated with the ASSR power and P1 component amplitude. A concurrent decrease in alpha power and increase in ERPs has been reported for the auditory N1 component during outside cycling Scanlon et al. (2019) and the auditory Mismatch Negativity component during riding a motorcycle (Vaughn et al., 2021). Work by Cao and Händel (2019) showed a co-modulation of overall alpha power and centrally visually entrained signals in different movement states. Only recently, a correlation between the visual N1 component and occipital alpha power modulation due to body movement was confirmed (Chen et al., 2022b). Based on this finding we had proposed that, as occipital alpha power likely marks an inhibitory process, inhibition may serve as a mechanism through which walking influences early sensory processing in visual tasks (Chen et al., 2022b). The work at hands supports and extends this idea to the auditory domain.

The strength of sensory entrainment is modulated by the walking path

By comparing the ASSR lateralisation index, which reflects the difference in the entrainment strength between left and right ear, a distinct pattern was observed between turns towards left and right. The pattern showed that the entrainment strength was dynamically modulated by the turning direction (see Figure ***4a***). Before the mid-turn was

603 reached, auditory processing was stronger at the side of the turn (e.g. a left turn increased
604 processing of left ear input) suggesting a stronger processing towards the side of the turn.
605 At mid-turn the entrainment was balanced between left and right, suggesting there was
606 no processing difference between left and right side with respect to the participant. After
607 mid-turn, processing was stronger at the opposite side of the turn.

608 The active sensing framework proposes that the motor system can influence
609 perception by directly generating sensory input through the execution of motor actions
610 (Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010; Yang, Wolpert, & Lengyel,
611 2018). In human walking and other natural behaviour, a number of studies has described
612 coordinated head and eye movements to gather visual input dependent on the features
613 of the surroundings and the specific geographic information related to the task (Hayhoe
614 & Ballard, 2005; Imai et al., 2001; Sprague & Ballard, 2003; Turano, Geruschat, & Baker,
615 2003). In such a way, active sensing shapes the specific content of sensory information
616 flowing from the bottom-up (Morillon, Hackett, Kajikawa, & Schroeder, 2015).

617 However, the current experiments delivered auditory stimuli via inserted
618 earphones (surpassing the threshold for perceiving other external auditory input),
619 ensuring that the auditory input remained unchanged regardless of the participants' head
620 position. Accordingly, even so we can assume a path-related modulation of head
621 movements, it was not the resulting change in auditory input that caused the path-specific
622 neural response modulation. We therefore propose a top-down mechanism to modulate
623 sensory processing during walking. The predictive coding theory suggest that the brain
624 creates predictions about sensory input based on past experiences and current goals and
625 that it is these predictions that guide sensory sampling and processing (Millidge, Seth, &

626 Buckley, 2021). A review of top-down control in the active sensing framework, particularly
627 with respect to rhythmic sampling, can be found in the work by Morillon et al. (2015).

628 In our experiments, the top-down modulation of sensory processing might be
629 realized via attentional processes. These attentional processes could potentially share
630 common neural circuitry with the systems governing eye and head movements. Previous
631 studies showed that focusing attention to a particular side led to enhanced ASSR power
632 in the corresponding side (Bharadwaj, Lee, & Shinn-Cunningham, 2014; Manting,
633 Andersen, Gulyas, Ullen, & Lundqvist, 2020; Ross, Picton, Herdman, & Pantev, 2004;
634 Skosnik, Krishnan, & O'Donnell, 2007; Voicikas, Niciute, Ruksenas, & Griskova-
635 Bulanova, 2016). Accordingly, the modulation of ASSR lateralisation observed in our
636 studies might reflect a shift of attention dependent on the walking path. This interpretation
637 suggests that active sensing goes beyond an active orchestrating of the sensors and
638 additionally includes a shift in attentional processes. Such behaviour might serve to
639 optimize navigation during natural walking. Our findings further suggest that such
640 attentional modulation due to walking extends to the auditory domain.

641 **Author contributions :** X.C. implemented the testing protocol, collected the data,
642 analysed the data, and wrote the manuscript. L.C. implemented the testing protocol, did
643 preliminary recoding and provided suggestions for data analysis and manuscript revision.
644 R.E.W analysed the data, provided suggestions for revising the manuscript. J.P.
645 contributed to technical equipment support. K.G. supported the development of the
646 project and revised the manuscript. B.H. developed the experiment, led the project, and

wrote the manuscript. All authors contributed significantly to the article and approved the submitted version.

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Figure Legends

Figure 1. The experimental set-up. (***a***) Movement Task: In experiment 1, there were three testing conditions: stepping, standing, and walking. In experiment 2, there were two movement conditions: standing and walking. In the standing condition, participants were instructed to stand in the centre of the marked walking pathway (indicated by a green dot). In the stepping condition, participants were asked to walk on the spot in the same location as in the standing condition. In 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 continuously played tones, intermittent burst tones lasting 100 ms were presented. Bursts could occur simultaneously in both the 39 Hz and 41 Hz tones, and participants reported hearing the bursts in a midline location, hence we termed it central burst. The burst could also occur 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. Participants were not instructed to respond to or attend to the tones in any particular way.

Figure 2. 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' ASSR power response for 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 alpha power response 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.

Figure 3. ASSR power and alpha power during different movement conditions. (***a***) The power between 35 and 45 Hz, averaged over fronto-central electrodes (AFz, Fz, F3, F4, Cz) 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 difference (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.

Figure 4. The ASSR lateralisation index is modulated by the walking path. (***a-b***) The ASSR lateralisation index 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 lateralisation 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 lateralisation 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***.

Figure 5. ASSR power perturbation induced by burst tones during walking compared to standing. (**a**) The ASSR power 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 power 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 power perturbation (left side ASSR) but not for the 41 Hz ASSR power perturbation (right side ASSR). (**e**) When the burst tone appeared on the right side, only the 41 Hz ASSR power 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. The green Asterisks* indicate $p < 0.05$.

Figure 6. 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 power perturbation (plotted in black) and 41 Hz power 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 power perturbation was statistically compared average over the time window between ([0 0.65]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).

Figure 7. 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 represent the time window of P1 ([150 200] ms) and P2 ([300 350] ms) component. (**b**) The modulation of the P1 amplitude (stand - walk) negatively correlated with the modulation of ongoing alpha power (stand - walk). (**c**) 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).