Spatial attention emerges from complementary modulation of the neural alpha rhythm and head movements

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Conflict of interest statement

The authors declare no conflict of interest.

Data accessibility

All data are available from the corresponding author upon request and will be made available on osf.io upon publication.

Abstract

The human brain is part of a moving body. However, almost all insights about the relationship between neural oscillations and cognition come from studies involving movement-constrained participants. Here, we test whether modulation of neural alpha oscillations (~10 Hz) and goal-directed head movements implement redundancy in guiding the focus of spatial attention. Human participants (*N*=33) listened to to-be-attended or to-be-ignored lateral sounds. Free head movements were allowed in half of the trials. We found two simultaneous attentional filter mechanisms. First, *neural filtering* showed up as decreased alpha power in the electroencephalogram (EEG) contralateral to targets and vice versa for distractors. Second, *behavioral filtering* was evidenced through gyroscopic tracking of head movements, which showed that listeners consistently turned the head towards lateral targets. Lateral distractors induced more variable movement patterns. Head rotations improved task accuracy by reducing target uncertainty and significant movement residues remained even when listeners were instructed not to move. To our surprise, trial-by-trial modulation of neural and behavioral filtering correlated positively, with lateralized alpha power sequentially interlocking with temporally delayed lateral eye movements and head rotations. We here see attention to emerge from sequential complementarity – rather than redundancy – of head movements with the neural alpha rhythm.

Significance statement

Cognitive neuroscience traditionally discards body movements as artifacts and, necessarily so, could not speak to their potentially integral role in cognition. We demonstrate a pivotal advantage from body movements in selective attention, a core cognitive function. Using mobile electroencephalography and gyroscopic tracking during auditory attention, we show that listeners rotate their heads towards relevant sounds, even when instructed not to, enhancing accuracy by reducing target uncertainty. Neural filtering, reflected in lateralized alpha oscillations, and behavioral filtering through head rotation were tightly linked in time and strength. Findings reveal that the foundation of attention is not purely neural but embodied—arising from interrelated neural and motor processes. Our results promote a reconceptualization of attention as a temporally interlocked brain–body process.

Introduction

Attention enables us to process relevant information despite competing distractions (Houghton & Tipper, 1994; Moore & Zirnsak, 2017; van Moorselaar & Slagter, 2020). Traditionally, cognitive (neuro)science has focused on uncovering how the mind and the brain implement attention, often treating overt body movements as unwanted noise (Nau et al., 2024; Stangl et al., 2023). However, to understand the basis of cognition, it is necessary to consider that the human brain evolved in a mobile body that can interact with the world (Reed & Hartley, 2021; Wilson, 2002). Although it is assumed that attention is not solely the outcome of internal neural computations but realized by overt actions, the mechanistic interplay of neural and motor processes to guide attention is largely unknown.

Movement-constrained laboratory studies have demonstrated the presence of *neural attention filters*, that is, brain mechanisms associated with target enhancement or distractor suppression (Desimone & Duncan, 1995; Kastner & Pinsk, 2004; Lakatos et al., 2013). A prominent spatial attention filter is the lateralization of inhibitory alpha oscillations at around 10 Hz, which decrease in brain areas processing targets and vice versa for distractors (Thut et al., 2006; Worden et al., 2000; Wöstmann et al., 2019; Yang et al., 2024). But is attention *embodied,* in the most literal sense of the word, in that body movements can improve attentional outcomes above and beyond what is known on neural mechanisms of attentional filtering? And if so, how does neural filtering interact with such body-implemented attention mechanisms?

Building on the concept of active sensing (Chen et al., 2025; Schroeder et al., 2010), we propose that body movements can act as *behavioral attention filters*. In vision, the frontal eye field has been implicated in both, covert shifts of attention and overt orienting via saccadic eye movements (Schall, 2004). Furthermore, attentional focusing in memory induces biases in gaze (van Ede et al., 2019, 2020) and head direction (Thom et al., 2023). Unlike other species, humans cannot move their ears to orient auditory attention. Yet, electromyographic recordings of the muscles that move the pinna have revealed slight increases in activity on the attended side (Strauss et al., 2020) – a possible relic of a behavioral attention filter.

A potent candidate for auditory filtering are head rotations, which are known to shape auditory scene analysis (Kondo et al., 2012) and enhance speech intelligibility in noise (Grange & Culling, 2016). Here, we use established criteria developed to define neural filters (Wöstmann et al., 2022) to probe auditory attentional filtering through head rotation.

In animals, strong links exist between body movement and neural dynamics (Musall et al., 2019) and between eye position and auditory neural responses (Groh et al., 2001). Furthermore, motor plans and attention recruit partially overlapping neural resources (Bello et al., 2025). Importantly, closing the eyes to focus on acoustic input modulates the effect of attention on alpha oscillations (Wöstmann et al., 2020) and oculomotor activity relates to alpha modulation during spatial attention (Liu et al., 2022; Popov et al., 2023), suggesting an interconnection of neural and motor processes involved in attentional selection.

Using mobile electroencephalography (EEG) combined with head-mounted gyroscopic tracking, we here examine participants' head rotation, neural oscillatory activity, and horizontal eye movements during a cued auditory spatial attention task. Neural and behavioral filtering are expected to serve the same goals—target enhancement and distractor suppression. We therefore hypothesized functional redundancy between the two filters, such that stronger recruitment of one would reduce the need for the other, manifesting as a negative correlation between them. Contrary, we here show that attention emerges from positive sequential interlocking of alpha

modulation with head rotations, demonstrating sequential complementarity rather than redundancy of neural and behavioral attention filters.

Results

Human participants (n = 33) were instructed to attend to one of two spoken numbers, presented simultaneously at two loudspeaker locations (front & left or front & right). The location of the target number was indicated by a fully valid visual spatial cue; the other number served as the distractor (Fig. 1). To equalize overall performance to ~50 % accuracy, the target-to-distractor sound intensity ratio (SNR) was adapted individually before the main experiment (M_{SNR} = –26.44 dB; SD_{SNR} = 3.13). No relationship was found between the adapted SNR and the head rotation results reported below. Participants had the task to report the target number on a number pad. The experiment was divided in eight blocks, during half of which participants were permitted to move their heads. To study attentional filtering in both, neural activity and patterns of head motion, we recorded electroencephalography (EEG) and head rotation using a head-mounted gyroscope.

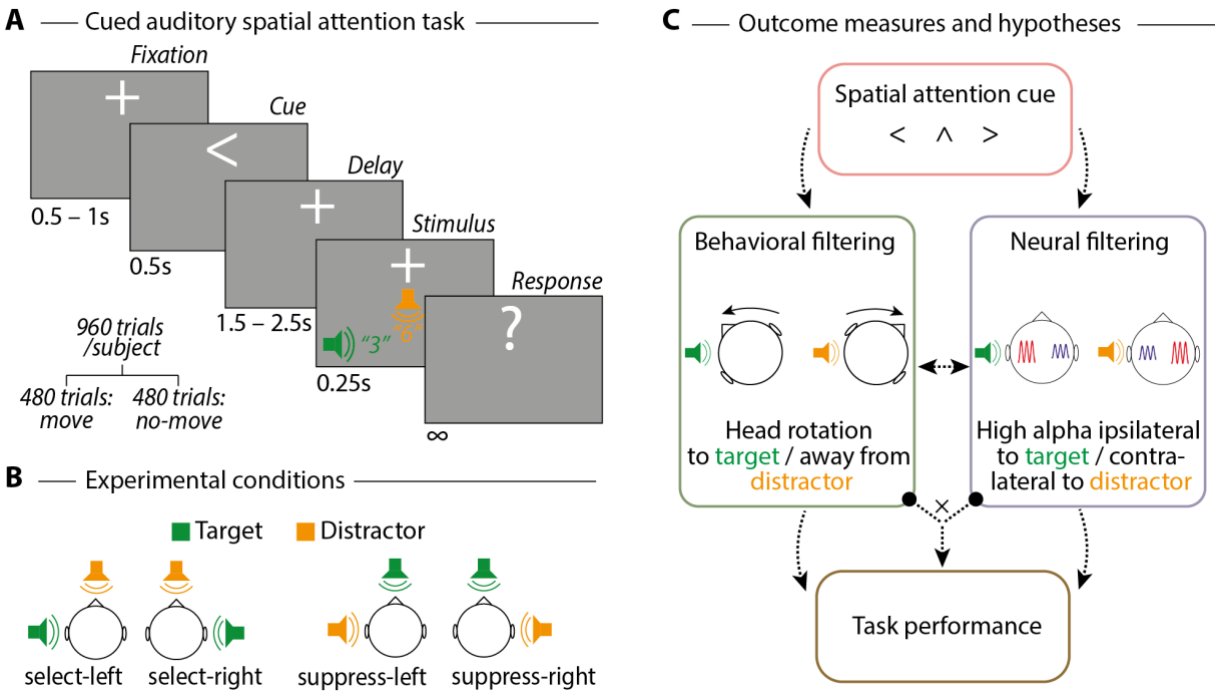

Figure 1. Study design and hypotheses. (**A**) Trial design of the cued auditory spatial attention task. (**B**) Experimental conditions (adapted from Wöstmann et al., 2019). (**C**) Schematic illustration of main outcome measures to assess behavioral attentional filtering (head rotation) and neural attentional filtering (lateralization of alpha oscillations). Dashed arrows indicate hypothesized relations tested in this study.

Top-down attention cues induce behavioral filtering. First, we asked whether participants would systematically employ head rotations as a filter mechanism for spatial attention. When head motion was permitted, cues indicating upcoming targets on the left or right side induced substantial head rotations towards the target (Fig. 2B; cluster p-value < .001; d = 0.832; cluster time window 0.23–2.08 s). Critically, we found an analogous, if markedly more low-amplitude, pattern of head rotation to lateral targets when movement was not permitted (cluster p-value = .001; d = 0.65; cluster time window 0.35–1.13 s). These results indicate that attention-related head

movements occur involuntarily, even under instructions to suppress overt actions, as is common in conventional, movement-restricted neuroscientific paradigms.

For lateral distractors, even though on average there was a trend for participants to rotate their heads away from the source of distraction, this pattern was not significant on the group level (Fig. 2C; move: all cluster *p*-values > .2; no-move: all cluster *p*-values > .5). However, this absence of a consistent group-level effect was not due to a general lack of head rotations when faced with lateral distractors. Instead, when movement was permitted, 18 out of 33 participants significantly rotated their heads away from the distractor, while 10 out of 33 participants significantly rotated their heads toward the distractor (Fig. 2D). This disparity suggests the use of different attentional filtering strategies to handle lateral distraction (for correlations of head rotation between conditions, see Fig. S1).

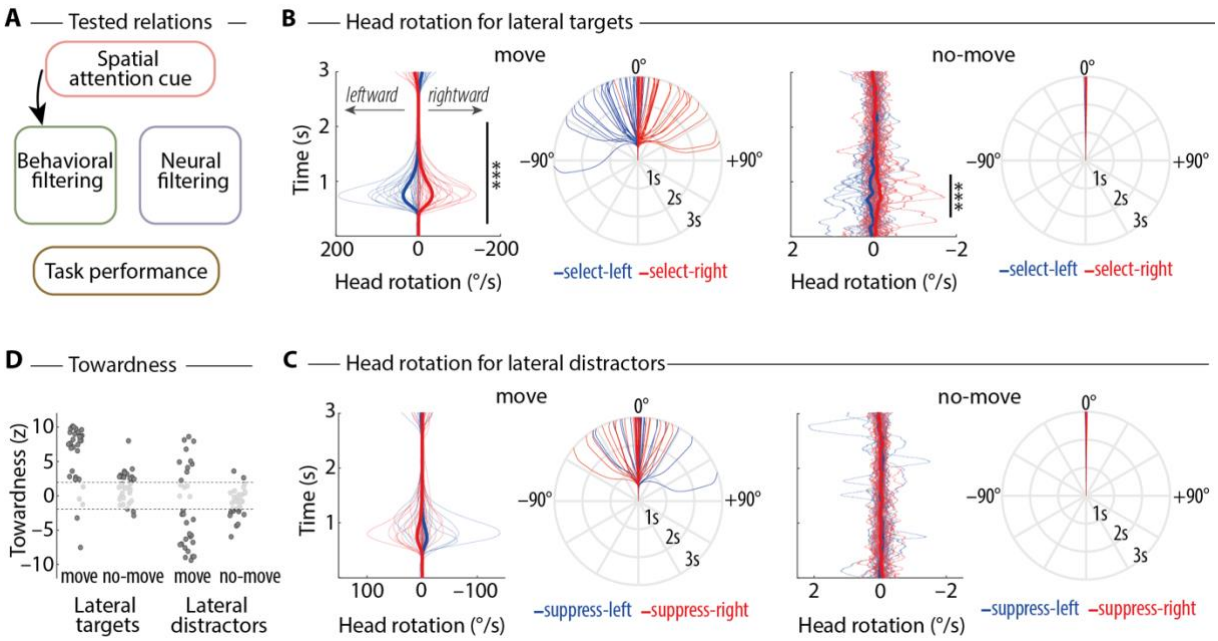

Figure 2. **Head rotation during auditory spatial attention**. (**A**) Overview of tested hypothesis (black arrow). (**B**) Line plots: Thin and thick lines show respective single-subject and average angular velocity of head rotation (around the yaw axis) for trials with (*move*; left) and without movement permitted (*no-move*; right). Black vertical lines and asterisks indicate significant differences for select-left versus select-right ($p < .05$; cluster-based permutation tests). Polar plots: Illustration of head orientation, calculated by integrating angular velocity over time. Note that absolute values of head rotation/orientation might be slightly underestimated due to tilt of the gyroscope, which was attached to the subjects' back of the head. (**C**) Same as B but for conditions with lateral distractors. (**D**) Towardness, calculated as the participant-specific *z*-contrast of angular velocity towards versus away from lateral targets/distractors (time window 0.35–1.13 s, i.e., overlap of significant clusters in B). Participants with no significant head rotation (i.e., $-1.96 < z < 1.96$) are masked. Note the bimodal distribution in the condition with lateral distractors and movement permitted.

Behavioral filtering improves task performance. Next, we asked whether and to what extent task performance would benefit from the permission to move the head. Across conditions, the proportion of correct responses was higher in blocks with ($M = 0.578$; $SE = 0.022$) versus without movement permitted (Fig. 3B; $M = 0.545$; $SE = 0.021$; main effect movement: $F_{1,32} = 35.5$; $p < 0.001$; $\eta_p^2 = 0.526$). This amounts to an average movement benefit of 3.27 percentage points (*k factor* = 1.1; Boothroyd & Nittrouer, 1988). Head motion was not equally beneficial across experimental conditions: While a movement benefit was absent in trials with the attentional target on the right side ($t_{32} = 0.18$; $p = 0.856$; $d = 0.032$; $BF_{10} = 0.19$), it was present for all other spatial arrangements

of target and distractor (select-left: t_{32} = 3.05; p = 0.005; d = 0.532; BF_{10} = 8.62; suppress-left: t_{32} = 3.77; p < 0.001; d = 0.657; BF_{10} = 46.61; suppress-right: t_{32} = 3.26; p = 0.003; d = 0.568; BF_{10} = 13.86). Furthermore, the permission to move enhanced confidence and reduced effort ratings (Fig. S2).

Independent of head movement, participants performed better in trials with lateral targets than lateral distractors ($F_{1,32}$ = 30.74; p < 0.001; η_p^2 = 0.49), which agrees with previous research (Dai et al., 2018; Wöstmann et al., 2019).

Having established head movement-related benefits for task performance, we next investigated *how* this movement benefit comes about. In our task, the proportion of erroneously reported distractors reflects attention capture by the irrelevant distractor. The proportion of erroneously reported non-distractors reflects target uncertainty (Fig. 3C). Including this factor of error type in the statistical analysis revealed a significant 4-way interaction with movement (no-move vs. move), loudspeaker setup (front & left vs. front & right), and role of lateral speaker (target vs. distractor; $F_{1,32}$ = 4.71; p = 0.038; η_p^2 = 0.128). Post-hoc tests revealed that the permission to move the head did not reduce distractor responses (t_{32} = –0.87; p = 0.39; d = 0.151; BF_{10} = 0.26) but non-distractor responses (t_{32} = –4.59; p < 0.001; d = 0.799; BF_{10} = 374.3). This movement-induced reduction of target uncertainty was consistent across conditions except for select-right trials, where movement was not beneficial (Fig. S3).

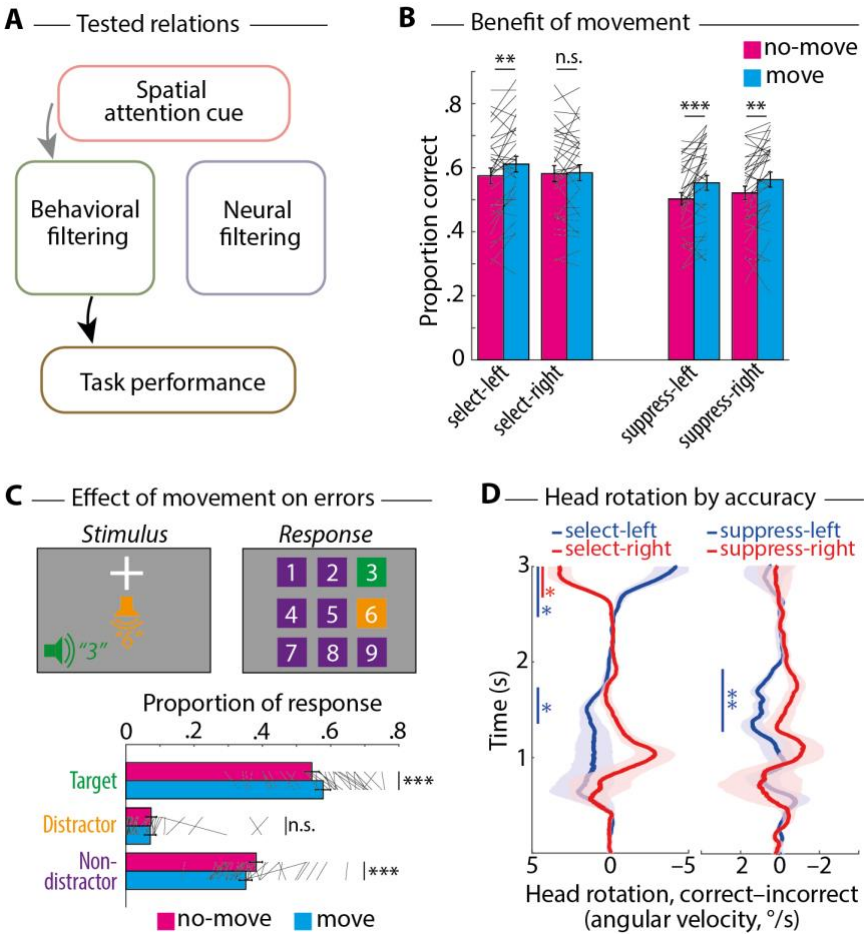

Figure 3. Relation of head rotation and task performance. (**A**) Overview of tested hypothesis (black arrow) and the previously established link (grey arrow). (**B**) Thin lines, bars and error bars show respective single-subject and average

of proportion correct ±1 SEM for different conditions. Black lines and asterisks indicate significantly higher accuracy for move versus no-move. (**C**) Grey boxes illustrate three different response types for a given trial (target, distractor, non-distractor). Thin lines, bars and error bars show respective single-subject and average proportion of response types ±1 SEM. (**D**) Lines and shaded areas show respective average angular velocity ±1 SEM for correct minus incorrect trials in conditions with movement permitted (for conditions without movement permitted, see Fig. S4). Vertical lines and asterisks indicate significant differences for correct versus incorrect trials, separately for targets/distractors on the left and right side ($p < .05$; cluster-based permutation tests). * $p < .05$; ** $p < .01$; *** $p < .001$; n.s. not significant.

Finally, we asked whether patterns of head rotation would differ for correct versus incorrect trials when movement was permitted. For trials with targets on the left, we found evidence for larger leftward head rotation in correct versus incorrect trials (Fig. 3D; cluster *p*-value = .045; *d* = 0.51 cluster time window 1.35–1.73 s). In addition, head rotation back to the center at the end of a trial was stronger for correct versus incorrect trials with targets on the left (cluster *p*-value = .014; *d* = 0.603 cluster time window 2.47–3 s) and on the right (cluster *p*-value = .02; *d* = 0.748; cluster time window 2.68–3 s). For trials with distractors on the left, participants rotated the head more to the left (i.e., in the direction of the distractor) when they reported the target number correctly versus incorrectly (cluster *p*-value = .002; *d* = 0.54; cluster time window 1.27–1.92 s). In sum, these findings provide evidence for the existence of the hypothesized link between behavioral filtering and task performance.

Neural signatures of attentional filtering also occur during free movement. Next, we tested whether the lateralization of alpha oscillations—a well-established neural signature of spatial attention in traditional, movement-constrained laboratory studies—would prove to be a robust metric of attention in conditions that closely resemble real life, including head movement.

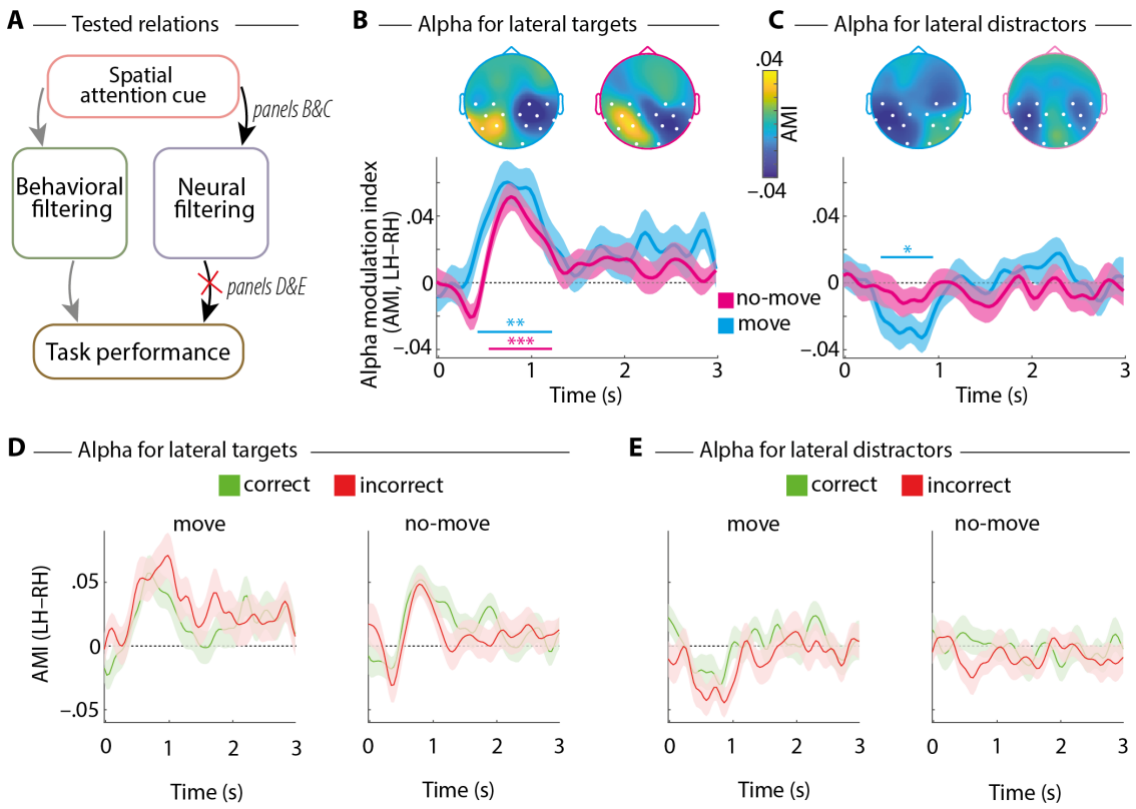

Figure 4. Lateralized alpha oscillations during auditory spatial attention. (**A**) Overview of tested hypothesis (black arrows) and previously established links (grey arrows). (**B**) The Alpha Modulation Index (AMI) for lateral targets was calculated on alpha (8-12 Hz) oscillatory power as: $AMI_{selection}$ = (select-left – select-right) / (select-left + select-right).

Lines show the average difference of AMI for the left – right hemisphere (LH–RH), separately for conditions with (blue) and without movement permitted (pink). Shaded areas show ±1 SEM. Horizontal lines and asterisks indicate significant temporal clusters for testing AMI against zero ($p < .05$; cluster-based permutation test). Topographic maps show AMI in time windows of significant clusters. White circles highlight electrodes used for calculating the hemispheric difference of AMI (LH–RH). (**C**) Same as B but for conditions with lateral distractors: $AMI_{suppression}$ = (suppress-left – suppress-right) / (suppress-left + suppress-right). Note that the topographic map for the no-move condition (where no significant cluster was found) refers to the same time interval as the significant cluster for the move condition. * $p < .05$; ** $p < .01$; *** $p < .001$. (**D&E**) Same as B&C but separately for correct (green) and incorrect trials (red). No significant clusters for the difference between correct and incorrect trials were found (all $p > .5$).

Well in line with the published literature (see Discussion), cues indicating a lateral target on the left or right side induced higher ipsi- than contralateral alpha power. Notably, however, this finding here proved robust against the permit to move the head (Fig. 4B): Cluster-based permutation tests revealed significant alpha lateralization for no-move and move conditions in similar time windows (no-move: cluster *p*-value = .002, *d* = 1.077; cluster time window 0.54–1.22 s; move: cluster *p*-value = .008, *d* = 0.794; cluster time window 0.42–1.22 s).

For trials with lateral distractors, alpha lateralization showed a significant reversed pattern (Fig. 4C; higher contra- than ipsilateral alpha power) for conditions with movement permitted (cluster *p*-value = .013, *d* = 0.64; cluster time window 0.38–0.94 s) but not for conditions without movement permitted (no clusters found). Importantly, alpha lateralization for lateral targets and distractors did not differ for no-move versus move conditions (all cluster *p*-values > .2), which demonstrates robust neural filtering in moving participants.

To test whether neural filtering would relate to improved task performance, we compared alpha lateralization for correct versus incorrect trials (Fig. 4D & E). No significant clusters were found (all cluster *p*-values > .5), which demonstrates that contrary to behavioral filtering, neural filtering did not relate directly to performance.

Relation of neural and behavioral filtering. Having established that cued top-down attention cues induce both neural and behavioral filtering, we ultimately asked whether and how these two filter mechanisms relate. For trials with lateral targets and movement permitted, alpha power lateralization increased with larger magnitude of head rotation (Fig. 5B, left; movement bin x hemisphere interaction: $F_{1.7,55.5} = 8.37$; $p = 0.001$; $\eta_p^2 = 0.207$; the interaction was not significant in other conditions, all $p > .4$). The same relationship showed up at the between-subject level, as individuals who on average performed larger head rotations exhibited more pronounced patterns of lateralized alpha oscillations (Fig. 5B, right; Spearman's *rho* = .413; *p* = .0175).

To investigate the temporal sequence of neural and behavioral filtering, we extracted the change in single-trial modulation of lateralized alpha power (i.e., first temporal derivative of left- versus right-hemispheric alpha amplitude) and the change in single-trial head position (i.e., angular velocity). Lateral eye movements have been associated with alpha power modulation (Liu et al., 2022; Popov et al., 2023) and typically precede head rotation (Stahl, 1999; Uemura et al., 1980). Despite the absence of eye-tracking data to assess microsaccades in the present study, the change in the single-trial horizontal electrooculogram (HEOG; i.e., first temporal derivative of amplitude difference at electrode F7–F8) was extracted to quantify lateral eye movements (Fig. 5C, left). Descriptively, on the group-level, changes in alpha-lateralization peaked first (~390 ms), followed by changes in HEOG (~490 ms) and changes in head orientation (~720 ms).

As per temporal cross-correlation at the single-trial level, the positive relation of lateralized alpha activity and head rotation was driven by stronger behavioral filtering following stronger

neural filtering with a temporal delay of ~375 ms (Fig. 5C, right; cluster *p*-value < .001; *d* = 0.751; cluster time window –0.57 to –0.18 s). This temporal delay was found invariably for correct and incorrect trials (Fig. 5D; all cluster *p*-values > .9 for potential accuracy differences).

Lastly, the data revealed a strong temporal co-occurrence of HEOG and head rotation, with eye-related activity preceding the head-related activity (Fig. 5C, positive cluster: *p*-value < .001; *d* = 0.924; cluster time window –1.5 to –0.01 s; negative cluster: *p*-value < .001; *d* = 0.889; cluster time window 0.1 to 1.5 s). Critically, no significant cross-correlation of lateralized alpha activity and HEOG was found (all cluster *p*-values > .09), which makes it unlikely that the observed relationship between alpha oscillations and head rotation is mediated by lateral eye movement activity.

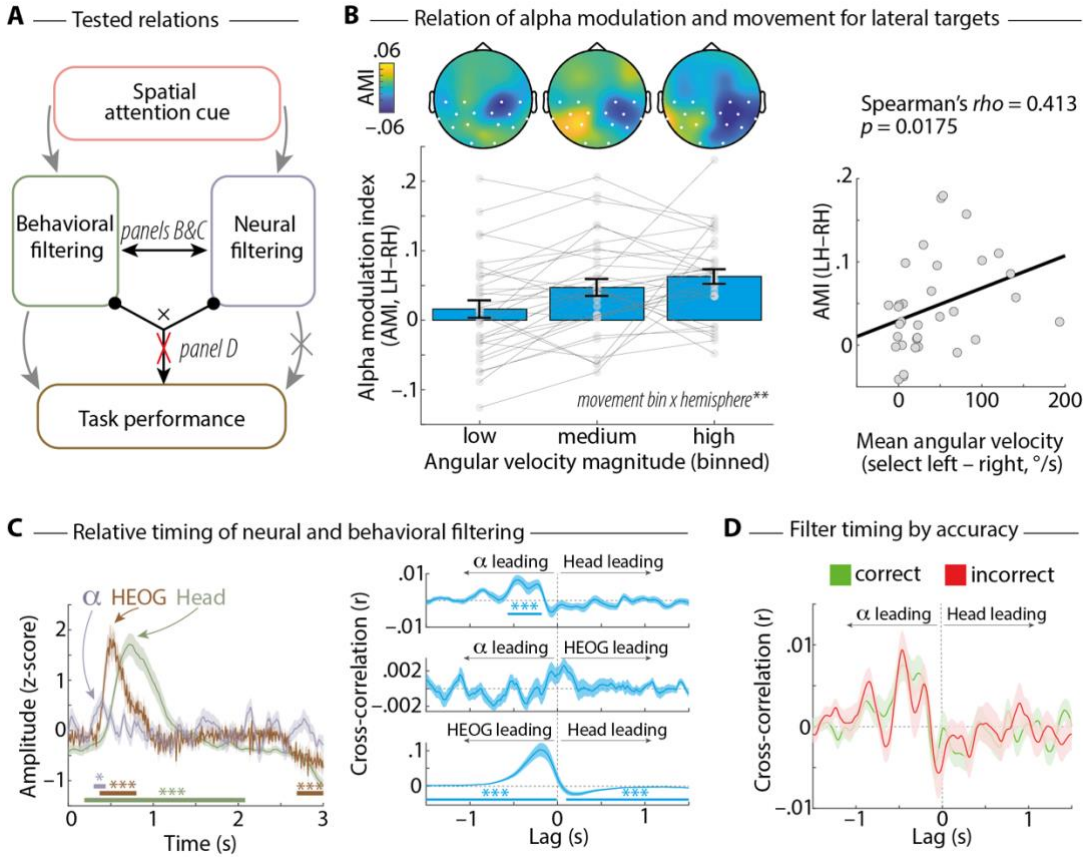

Figure 5. Relation of neural and behavioral filtering. (**A**) Overview of tested hypothesis (black arrows) and previously established links (grey arrows). (**B**) Bars, error bars, and lines show respective mean ±1 SEM and single-subject alpha modulation index (AMI) for the left – right hemisphere (LH–RH), binned for the magnitude of angular velocity (time window AMI: 0.42–1.22 s; time window head rotation: 0.35–1.13 s). Data are shown for trials with lateral targets and movement permitted. Topographic maps show the average AMI, binned for angular velocity. ** Significant movement bin x hemisphere interaction (*p* < .01). The scatterplot shows individual participant's AMI (LH–RH; time window: 0.42–1.22 s) by mean angular velocity (time window: 0.35–1.13 s), including the least-squares regression line. (**C**) Left: For conditions with lateral targets and movement permitted, we calculated single-trial neural filtering (1st temporal derivative of $AMI_{single\text{-}trial}$), behavioral filtering (angular velocity), and the horizontal electrooculogram (HEOG; 1st temporal derivative of amplitude difference at electrode F7–F8). For visualization, since all three measures are supposed to reverse amplitude depending on the side of the lateral target, they were multiplied by –1 in select-right trials, followed by averaging across trials and z-scoring. Lines and shaded areas show mean ±1 SEM, respectively. Horizontal lines and asterisks indicate significant clusters for tests against zero (*p* < .05; cluster-based permutation test). Right: Mean ±1 SEM of single-trial pairwise cross-correlations. Horizontal lines and asterisks indicate significant clusters for tests against zero. (**D**) Same as C (right, upper panel) separated for trials with correct (green) versus incorrect responses (red), which did not differ significantly (all cluster *p*-values > .9). * *p* < .05; ** *p* < .01; *** *p* < .001.

Discussion

In this study, we demonstrate that head rotations pose a powerful behavioral filter mechanism that engenders auditory attention, above and beyond the well-studied attentional modulations of brain activity. First, behavioral filtering improves task accuracy by reducing uncertainty about the attentional target while neural filtering does not. Second, behavioral filtering is ubiquitous, as listeners perform miniature head rotations to lateral targets even when instructed not to. Third, behavioral filtering relates positively to temporally preceding modulation of lateralized alpha oscillations, suggesting that spatial attention emerges from sequential complementarity—instead of redundancy—of head movements and the neural alpha rhythm.

Behavioral filtering emerges as a core component of attention. Previous research has shown that listeners' head movements benefit auditory scene analysis and speech comprehension in noise (Grange & Culling, 2016; Kondo et al., 2012). Acoustic differences of competing sounds arriving at the two ears facilitate detection and identification – a phenomenon called *binaural unmasking* (Culling & Lavandier, 2021; Kock, 1950). Head movements modulate binaural unmasking, with rotations of ~30° being acoustically optimal for lateral targets (90°) and noise in front (0°; Hládek & Seeber, 2023; Jelfs et al., 2011). Additionally, movement might support cognitive offloading (Risko & Gilbert, 2016), that is, the use of physical action (i.e., head rotation) to reduce cognitive demand (i.e., keeping track of where to focus attention). Here, we demonstrate that preparatory attention cues induce systematic head rotations in the direction of upcoming lateral targets, thus implementing an endogenous, proactive attentional filter (Geng, 2014).

Head rotations towards lateral targets were still evident when participants were instructed not to move, albeit reduced by approximately two orders of magnitude. This suggests that head rotations were planned but inhibited (Tcaci Popescu & Wexler, 2012). This is reminiscent of microsaccades towards targets in covert visual spatial attention (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Liu et al., 2024). Thus, head rotations emerge as a filter mechanism that is not fully suppressed on command, demonstrating their ubiquity. This suggests that planning and carrying out (miniature) head movements may interact with neural recordings and task accuracy, even in movement-constrained spatial attention investigations. However, this remains unexplained if head movements are not considered.

Permission to move the head improved target speech reception by ~3.3 %. The lack of an improvement for target speech on the right side was unexpected, but could be due to a right ear advantage for speech (Hiscock & Kinsbourne, 2011; Kimura, 1961), which might mitigate the benefits of head rotation. Performance-beneficial head rotations to the left for targets and distractors on the left side suggest that listeners employed head rotations to enhance target sampling and segregate targets from distractors, respectively. These effects might underestimate the impact of head rotations in real life to some extent, as our design implemented a limited number of spatial loudspeaker arrangements and thus induced stereotypical patterns of head rotation, which likely reduced the variance across (correct versus incorrect) trials.

A hallmark of contemporary attention research is to separate filter mechanisms related to target enhancement from distractor suppression (Noonan et al., 2018; van Moorselaar & Slagter, 2020; Wöstmann et al., 2022). Convergingly, our findings suggest that head rotations are primarily employed to modulate target processing. On the group-level, significant head rotations were found in the direction of lateral targets but not away from lateral distractors. The observed heterogeneity of head rotations in the case of lateral distractors might suggest that some listeners rotated their head towards lateral distractors to increase initial distractor sampling to support

ensuing suppression (Moher & Egeth, 2012), or to increase the signal-to-noise ratio on the ear closer to the target (i.e., better-ear listening; Edmonds & Culling, 2006; Kokabi et al., 2019). Another group of listeners rather reduced the overall sampling of the distractor by turning the head away. Furthermore, when permitted to move the head, the number of errors associated with target-distractor confusions remained the same, indicating that head rotations do not help to suppress attention capture of the distractor (Dalton & Hughes, 2014). Instead, the permission to move improved accuracy by reducing reports of items that were neither targets nor distractors, suggesting a behavioral filtering-induced reduction in target uncertainty.

Behavioral and neural filtering: complementary roles towards a common goal. This study sets the stage for a research program that integrates goal-directed body movements in the neuroscience of attention. In line with movement-constrained laboratory studies, we found that spatial cue-induced lateralization of alpha oscillations reflects the focus of auditory spatial attention (Ahveninen et al., 2013; Müller & Weisz, 2012; Wöstmann et al., 2019). Relatively reduced versus enhanced alpha power contralateral to a target versus distractor is thought to relate to neural enhancement versus suppression, respectively (Schneider et al., 2021), but the link to behavioral filter mechanisms is unclear. Analogous modulation of neural alpha oscillations in conditions that permit and exclude movement demonstrates that neural and behavioral filter mechanisms are not strictly dependent on each other.

Neural and behavioral filters appear to contribute differently to spatial attention. Contrary to head rotation, alpha lateralization did not relate to improved task accuracy. Brain stimulation studies found evidence for causal contributions of lateralized alpha oscillations to auditory (Deng et al., 2019; Wöstmann et al., 2018) and visual spatial attention performance (Kasten et al., 2020; Kemmerer et al., 2022). However, recent work casts doubt on the view that lateralized alpha oscillations modulate target versus distractor processing in early sensory areas (Brickwedde et al., 2025; Gundlach et al., 2020; Zhigalov & Jensen, 2020), suggesting that spatial shifts of attention induce alpha modulation, not vice versa (Antonov et al., 2020). Here, we demonstrate how investigating a second filter of attention — behavioral filtering — helps understanding the function of neural filtering via lateralized alpha oscillations.

Recordings of neural activity alone reveal descriptions rather than explanations (Krakauer et al., 2017). Increased alpha power has been interpreted to reflect the intention to resist a contralateral distractor (Bonnefond & Jensen, 2024). Including recordings of behavioral filtering, our findings suggest that this is only partly the case. A considerable number of participants aimed to achieve filtering by separating the target from the distractor perceptually, thereby turning their heads towards instead of away from a lateral distractor. Thus, considering behavioral filter mechanisms is inevitable if the goal is to explain the purpose of attentional filtering.

Furthermore, behavioral filtering helps understand the reference frame (Zaehle et al., 2007) of attention-induced modulation of parietal alpha oscillations. If alpha lateralization codes the spatial focus of attention with respect to momentary head direction (i.e., head-centered or egocentic; Town & Bizley, 2022), head rotations should subsequently induce a modulation of neural filtering—which is not what we found. Instead, alpha modulation preceded head rotation and, importantly, retained its scalp-lateralized and temporal profile for conditions with and without permitted head movement. This result is rather in line with neural attentional filtering coding the focus of spatial attention in more allocentric or at least movement-invariant terms, with respect to the initial head direction at trial start.

Coupling and timing of neural and behavioral filters. The primary objective of the present study was to examine the relationship between neural and behavioral filtering as a means of probing the mechanistic implementation of spatial attention. While no relation would suggest independent filter mechanisms, a negative relation would indicate *redundancy*, where stronger recruitment of one filter reduces the need for the other. Instead, we discovered a temporally ordered, positive association indicating *sequential complementarity*.

Modulation of lateralized alpha activity temporally preceded positively related changes of head rotation by 300–400 ms, corresponding to a delay of 3 to 4 alpha cycles. This speaks against the possibility that head movement-related activity drives lateralization of alpha oscillations. Given the complementary roles of neural and behavioral filtering explained above, our results support an embodied model of attention (Bruineberg & Stone, 2024; Reed & Hartley, 2021) wherein a common upstream attention signal independently initiates neural alpha power modulation and head rotation, with the former reflecting the neural coding of relevant and irrelevant information in space and the latter modulating the sampling of sensory input to improve target processing.

Overlapping motor and attention systems in frontal cortex regions (Bello et al., 2025; Schall, 2004) might constitute a potential source of attention signals driving neural and behavioral filtering. Furthermore, the superior colliculus is involved in shifting spatial attention (Ignashchenkova et al., 2004) and contributes to head movements (Gandhi & Katnani, 2011). Also, Oculomotor activity might affect the interplay of neural and behavioral filtering, as it relates to lateralized alpha oscillations (Liu et al., 2022; Popov et al., 2023) and precedes head rotation (Stahl, 1999; Uemura et al., 1980). However, in the present study, lateral eye movements related to temporally lagging head rotation but not to modulation of neural filtering. Thus, our findings do not suggest a central role of lateral eye movements in orchestrating the relation of neural and behavioral filtering (but note that microsaccades were not assessed here).

Conclusion

Spatial selective attention relies on the coordination of complementary neural and behavioral filtering: Modulation of the parietal alpha rhythm codes spatial relevance, while head rotations implement overt sampling that improves performance by reducing target uncertainty. The temporally ordered coupling of neural alpha oscillations and over actions suggests coordinated control through a common upstream mechanism. This research invites models that treat overt movement as an integral component of cognitive control.

Methods

Participants. N = 33 human participants took part in the present study (26 females & 7 males; 32 right-handed & 1 left-handed; M_{age} = 23.15 years; SD_{age} = 2.97). Data of 7 additional participants were recorded but not used in the analysis due to missing data or technical problems. Participants provided written informed consent and were compensated for participation financially or with course credit. All experimental procedures were approved by the local ethics committee of the University of Lübeck.

Stimulus materials and task design. Auditory stimuli were German numbers 1–9, spoken by a female voice (Wöstmann et al., 2017). Numbers were shortened to 250 ms duration (using Praat 6.2.22) and overall sound intensity was equalized.

The cued auditory spatial attention task (Fig. 1) was adopted from previous studies (Wöstmann et al., 2019, 2025). One loudspeaker (Genelec 8020D) was placed in front of the participant (0°; ~85 cm distance; above the monitor). The other loudspeaker was either placed on the left or right side (i.e., –90° or +90°; ~85 cm distance). On each trial, one loudspeaker was the cued target and the other was the distractor, implementing two conditions with lateral targets (*select-left*, *select-right*) and two conditions with lateral distractors (*suppress-left*, *suppress -right*).

Each trial started with a baseline wherein a fixation cross was presented (500–1000 ms, randomly jittered in 10-ms steps). Next, a visual spatial cue appeared (500 ms; arrow hat pointing left, right, or front). During the ensuing delay period, the cue changed to a fixation cross (1500–2500 ms, randomly jittered in 1-ms steps). Then, the auditory stimulus was presented, which consisted of two different numbers, each presented at one loudspeaker location (front-left or front-right; duration: 250 ms). After stimulus presentation, the response screen appeared, showing a question mark. Participants had to report the number presented at the cued location using a number pad. There was no time out for the behavioral response.

Each participant performed 960 trials, separated in 8 blocks à 120 trials. In half of the blocks, participants were allowed to move their head, while movement was discouraged in the other half. The instruction to move / not move alternated from every block to the next. The loudspeaker setup (front–left vs. front–right) changed after every two blocks (participants with odd and even IDs started with front–left and front–right, respectively). For all trials in a block, the cue direction (front vs. side) varied randomly with the constraints that each cue appeared on half of the trials and that no cue would repeat more than three times. For every combination of setup (front–left vs. front–right) and movement (move vs. no-move) there were 2 blocks. For each participant, we randomly selected 240 pairs of target and distractor numbers and used these in randomized order for every combination of setup and movement.

Individual stimulus adjustment. Before the main experiment, the individual signal-to-noise ratio (SNR) for target and distractor stimuli was determined to achieve accuracy of around 50 % (using the Palamedes toolbox for Matlab; Prins & Kingdom, 2018). Target numbers were presented in front and distractors either on the left or right side. A one-up, one-down adaptive staircase procedure was used (Levitt, 1971). The staircase started with an SNR of +4 dB and was lowered vs. raised by 2 dB after each correct vs. incorrect response, respectively. The staircase terminated after 50 trials. The average SNR across the last four reversals was used for all conditions of the main experiment. Movement was discouraged during the stimulus adjustment phase.

Recording and analysis of head motion data. Head motion and the electroencephalogram (EEG) were recorded with a mobile EEG system (Smarting PRO Indoor, mBrainTrain, Belgrade) and digitized at 500 Hz. Head rotation was measured in angular velocity (°/s) around three orthogonal rotational axes (yaw, pitch, roll). Additionally, acceleration along the three axes was assessed (m/s^2), but not analyzed for the purpose of the present study.

To quantify horizontal head rotation to the left vs. right side, single-trial rotation around the yaw axis was extracted and averaged across trials, separately for experimental conditions. Other rotational axes (pitch & roll) were inspected as well but showed negligible variation as a function of experimental conditions. To calculate head orientation, angular velocity was integrated over time, using the function *cumtrapz* in Matlab. Of note, due to the placement of the amplifier box hosting the gyroscope on the neck, the gyroscope was somewhat tilted for most participants. Thus, absolute rotational angles around the yaw axis underestimate the true rotation to some extent.

We adopted a measure of towardness from previous research on gaze bias (van Ede et al., 2020) to express single-subject head rotation toward versus away from lateral targets/distractors. Therefore, the contrast was calculated of angular rotation in trials with the lateral stimulus on the left versus right side (time window: 0.35–1.13 s) as a standardized *z*-value.

Recording and analysis of EEG data. The EEG was recorded at 32 electrodes (Ag/AgCl; 10-20 placement), using a common mode sense (CMS) reference and a driven right leg (DLR) ground. All electrode impedances were below ~10 kΩ. To ensure equivalent placement of the EEG cap, the vertex electrode (Cz) was placed at 50% of the distance between inion and nasion and between left and right ear lobes. For EEG preprocessing and analysis, we used the FieldTrip toolbox for Matlab (Oostenveld et al., 2010). Offline, the data were cut in epochs of –1 to +5 s around cue onset and filtered between 0.3 (high pass) and 100 Hz (low pass). An independent component analysis (ICA) was used to inspect and remove artefactual components based on component time courses, topographic maps, and spectra (average number of removed components: 17.21 of 32; SD: 3.88). Next, 10 % of trials with largest ranges at any channel in the time interval –0.2 to +2.5 s around cue onset were removed and the data were re-referenced to the average of all channels. Trials were then split into experimental conditions and time frequency representations were derived using complex Fourier coefficients for a moving time window (fixed length of 0.5 s; Hanning taper; moving in steps of 0.04 s) for frequencies 1–80 Hz with a resolution of 1 Hz and 2-Hz spectral smoothing.

To quantify neural filtering, two previously established alpha modulation indices (AMI) were calculated on oscillatory power in the 8–12 Hz band (Wöstmann et al., 2019). To quantify neural selection of lateral targets, we calculated $AMI_{selection} = (Pow_{select\text{-}left} - Pow_{select\text{-}right}) / (Pow_{select\text{-}left} + Pow_{select\text{-}right})$. To quantify neural suppression of lateral distractors, we calculated $AMI_{suppression} = (Pow_{suppress\text{-}left} - Pow_{suppress\text{-}right}) / (Pow_{suppress\text{-}left} + Pow_{suppress\text{-}right})$. AMIs were then contrasted for eight electrodes on the left (C3, T7, CP1, CP5, TP9, P3, P7, O1) vs. right hemisphere (C4, T8, CP2, CP6, TP10, P4, P8, O2).

Relative timing of neural and behavioral filters. Changes in head orientation (i.e., head rotation in °/s) around the yaw axis were extracted for single trials. To compute single-trial alpha lateralization, preprocessed single-trial EEG data were high-pass– and low-pass–filtered at 8 and

12 Hz, followed by computation of the alpha band envelope (ENV; using the *envelope* function in Matlab) for eight electrodes on the left (LH) and eight electrodes on the right hemisphere (RH). Next, we averaged across electrodes within each hemisphere and calculated the $AMI_{single\text{-}trial} = (ENV_{LH} - ENV_{RH}) / (ENV_{LH} + ENV_{RH})$, followed by calculation of the first temporal derivative to quantify changes in alpha lateralization.

To detect lateral eye movements in the single-trial raw (unprocessed) EEG signal, we applied a 100-Hz low pass filter and baseline-corrected the data by subtraction of mean amplitude in the time interval –0.1 to 0 s. Then, we calculated the amplitude difference at electrode F7–F8 (see also Lins et al., 1993) to estimate the horizontal electrooculogram (HEOG), followed by computation of the first temporal derivative.

The three single-trial measures (head rotation, AMI_{single_trial}, HEOG) were resampled to 100 Hz and extracted in the time interval 0–3 s, relative to cue onset. Pairwise cross-correlations between single-trial measures were calculated using the *xcorr* function in Matlab.

Statistical analyses. Average proportion of correct responses per condition and participant were transformed to rationalized arcsine units (rau) and submitted to repeated-measures ANOVAs followed by post-hoc *t*-tests. For dependent-samples *t*-tests, we report Cohen's *d* effect size; for repeated-measures ANOVAs, we report partial eta-squared (η_p^2). To test for significant neural and behavioral filtering across time, we applied cluster-based permutation tests (Gerber, 2025; two-sided, 10,000 permutations) on angular velocity and alpha lateralization indices (AMI), respectively. Cohen's *d* effect sizes for cluster tests were derived from dependent-samples *t*-tests calculated on the data in the time intervals of significant clusters.

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Supplementary materials

for

Spatial attention emerges from complementary modulation of the neural alpha rhythm and head movements

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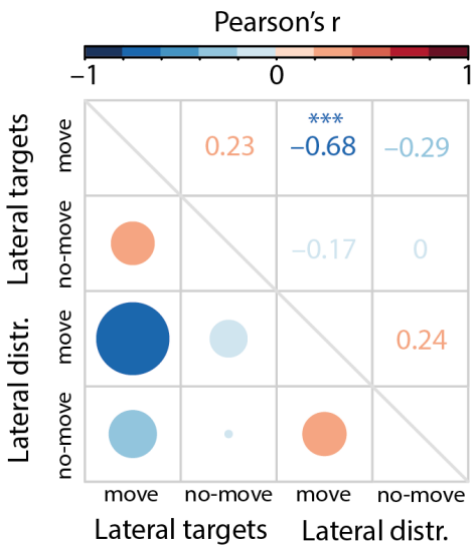

Figure S1. Heatmap shows Pearson' r for pairwise correlations of single-subject head rotation (i.e., Towardness shown in Fig. 2D in the main manuscript). Note that only the correlation between the two movement conditions was significant (lateral targets, move & lateral distractors, move; $r = -0.6794$; $p < 0.001$), indicating that participants who moved more significantly in the direction of lateral targets also moved more significantly away from lateral distractors.

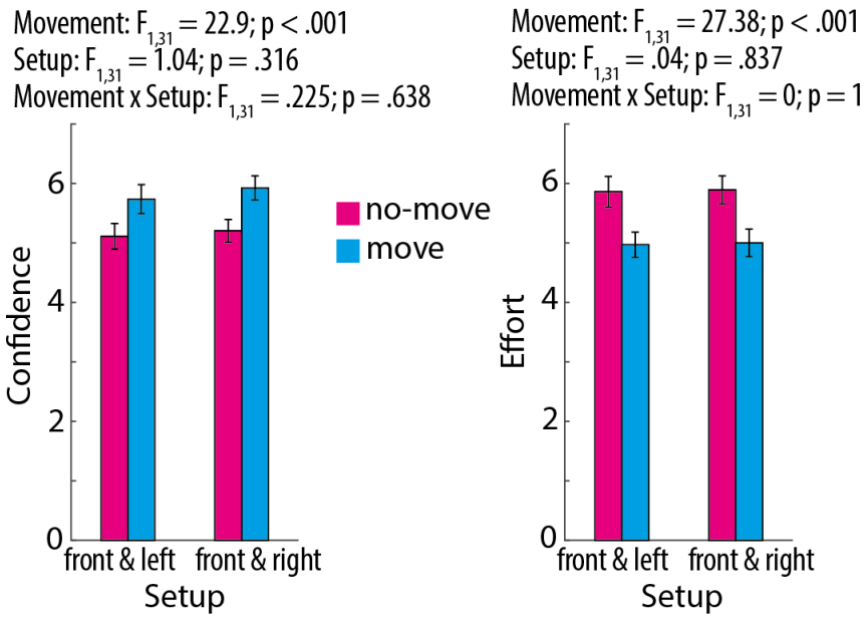

Figure S2. Confidence and effort ratings were collected in the end of each block on a scale from 1 (very low confidence / very low effort) to 10 (very high confidence / very high effort). Confidence was probed with the item "How confident are you that you reached a good performance level in this block?" Effort was probed with the item "How effortful did you experience the listening task in this block?" Results of two-way repeated measures ANOVAs with the factors movement (move vs. no-move) and loudspeaker setup (front & left vs. front & right) are shown above bar graphs. Bars show mean confidence/effort, error bars show ±1 SEM. Irrespective of the speaker setup, confidence ratings were significantly higher and effort ratings lower for blocks with movement permitted.

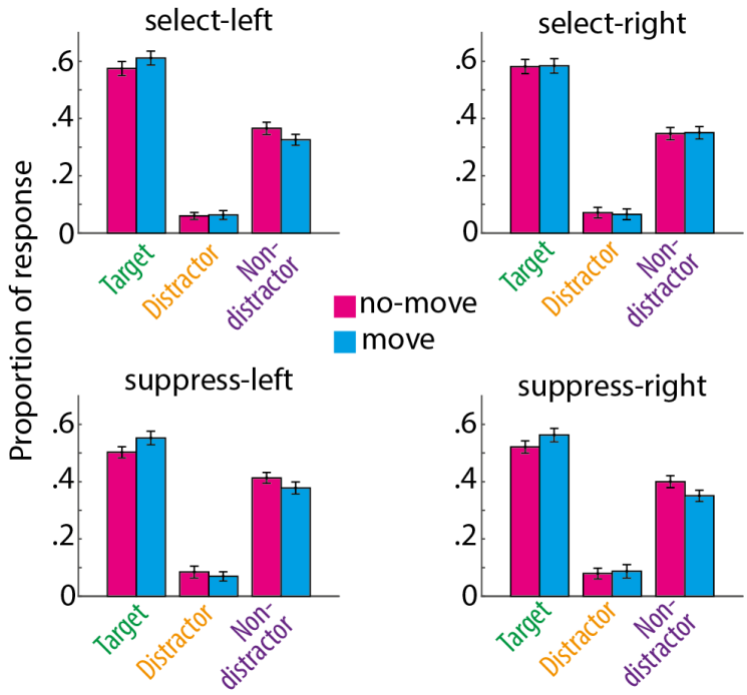

Figure S3. Bars show average proportion of responses for different response types for the four different experimental conditions. Error bars show ±1 SEM.

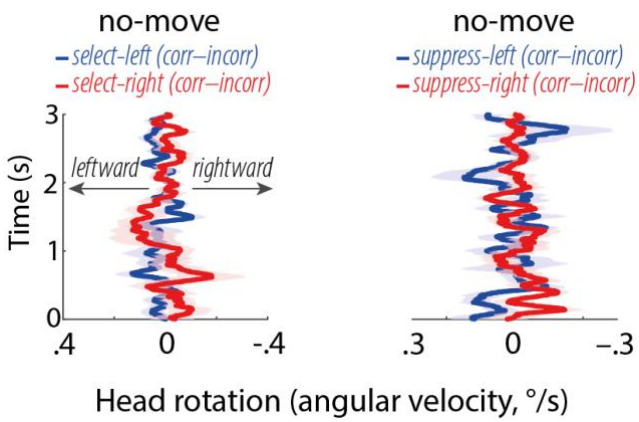

Figure S4. (**Left**) Lines and shaded areas show average angular velocity ±1 SEM for the difference of correct versus incorrect trials for trials with lateral targets and without movement permitted. (**Right**) Same as left but for trials with lateral distractors. No significant differences between correct and incorrect trials were found for these conditions (all $p > .05$, cluster-based permutation tests).