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Backward alpha band oscillations shape perceptual bias under probabilistic cues

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Predictive coding theory suggests that prior knowledge is crucial for optimizing human decision-making. However, how cortical dynamics implement this integration remains unclear. Here, we employ a traveling wave approach to investigate how alpha band oscillations integrate prior expectations during a perceptual decision-making task. Our findings demonstrate that expectation-based knowledge triggers the propagation of alpha band traveling waves from frontal to occipital areas, with this increase associated with enhanced modulation of brain regions involved in stimulus processing and directly linked to prior-driven bias at the behavioral level. Moreover, participants who rely more on prior expectations exhibit stronger top-down signaling (frontal-to-occipital), whereas those who focus on sensory input show a contrasting bottom-up pattern (occipital-to-frontal). These results highlight the role of alpha band traveling waves in predictive mechanisms, suggesting that rhythmic interactions across brain regions facilitate this process and contribute to inter-individual differences in its implementation.

The brain's capacity to generate predictions plays a pivotal role in perception and decision-making[1]. Predictive coding theory proposes that the brain continuously generates expectations about incoming sensory information based on prior knowledge, forming an "internal model" to interpret the sensory world[2]. Predictive processing relies heavily on top–down information flow, whereby higher-order cortical areas send signals to lower-level regions[3,4]. Such signals modulate sensory systems to refine perceptual experiences based on the probabilistic structure of the environment. This modulation, in turn, leads to shifts in perceptual parameters, including reaction time, decision criteria, and decision confidence[5–10]. Neural oscillations, particularly in the alpha band (8–14 Hz), are understood to play a critical role in coordinating these top–down modulations. Traditionally associated with attentional and inhibitory functions[11–18], alpha band activity is hypothesized to also support predictive processing by conveying top–down information flow across the cortical hierarchy[19]. Specifically, alpha rhythms appear to adapt the decisional process in alignment with environmental expectations, modulating responses according to probabilistic cues and fostering perceptual and behavioral adaptations. For example, we demonstrated that the modulation of parieto-occipital alpha band amplitude underpins probabilistic cue integration into perceptual processing[20]. Additionally, Kloosterman et al. [21] showed that posterior alpha band amplitude modulation serves to strategically bias evidence accumulation during perceptual tasks. Moreover, it accounts for the modulation of both criterion[22] and confidence levels in the response[23–25].

Crucially, alpha oscillations are not static but can flow as "traveling waves" across cortical areas, propagating from one region to another in a specific direction (e.g., anterior to posterior or vice versa). These traveling waves are thought to facilitate efficient signal transmission between brain regions, supporting broad cortical communication[26–29]. Within a predictive coding framework, alpha band traveling waves may convey prediction-based information from higher-order brain regions toward areas specializing in sensory processing, thereby preparing the perceptual system for upcoming stimuli. The directionality of these waves would be particularly revealing in this domain: while forward-directed waves (posterior-to-anterior) are particularly enacted during sensory stimulation[11,30,31], backward-directed waves (anterior-to-posterior) may reflect a predictive signal moving from higher-order areas to sensory areas in order to shape responses based on expectations.

Here, we investigated the role of alpha band traveling waves in incorporating predictive information into perceptual decision-making. We used a visual detection task in which human observers viewed visual stimuli preceded by probabilistic cues that suggested the likelihood of target appearance. Drawing from our previous research[20,32], we hold that these cues significantly influence participants' decision criteria, serving as a robust means of understanding how probabilistic expectations are integrated into perceptual judgments. Using EEG, we analyzed alpha oscillations as traveling waves to understand how this predictive information affects perception in the task at hand. Specifically, we focused on

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alpha band wave directionality in brain regions contralateral to the expected stimulus. We aimed to determine whether backward-traveling alpha band waves could serve as carriers of probabilistic information, thereby modulating participants' perceptual decisions accordingly. Furthermore, we investigated whether individual differences in the effects of priors on perception were underpinned by distinct modulation of traveling waves.

Our findings reveal a significant increase in backward alpha band waves following cue induction in the contralateral hemisphere during the prestimulus period. This contralateral lateralization suggests that backward alpha band waves serve as a means of conveying predictive information to the brain regions responsible for stimulus processing, effectively preparing the perceptual system for stimulus anticipation. Additionally, our results demonstrate a robust link between the modulation of decision criteria at the behavioral level and the power of these backward alpha band waves. Participants exhibiting stronger backward-traveling alpha band waves showed a greater likelihood of integrating predictive information from the cues into their perceptual decisions, adjusting their decision criteria in alignment with the cue's predictions.

These results provide compelling evidence for the role of backward alpha band traveling waves in integrating probabilistic cues into perceptual decision-making. By supporting the transmission of predictive information to sensory-processing regions, alpha band waves appear to facilitate a dynamic interaction with environmental cues. This dynamic modulation supports strategic decision-making, underscoring the crucial function of alpha rhythms in aligning perceptual systems with the brain's predictive model.

Results

Probabilistic cues shape the decisional criterion

Eighty healthy participants performed a detection task (Fig. 1A). In each trial, a checkerboard pattern appeared in the lower left visual field, which either included isoluminant gray circles within its cells (target trials) or did not (catch trials). Participants were asked to respond using the keyboard to

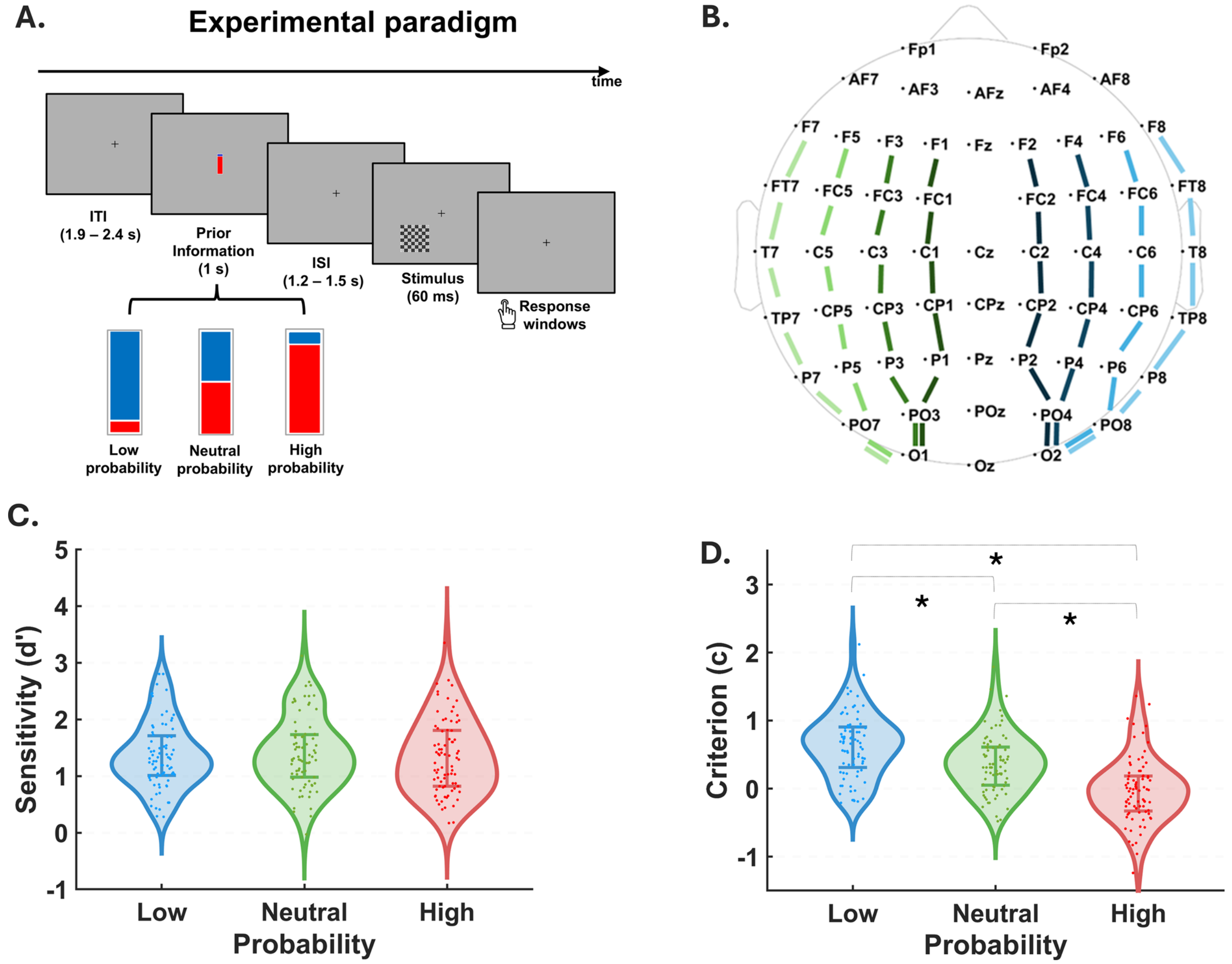

Fig. 1 | Experimental setup and behavioral results. A EEG data were collected during a basic visual detection task ($N = 80$). Each trial started with a fixation cross, followed by a probabilistic cue in the center of the screen. A checkerboard then briefly appeared (60 ms) in the lower left corner, which could contain gray circles at a set contrast level. The cue was a rectangular bar, with red on the bottom and blue on top, indicating target probability based on the color ratio. The task included three probability levels: high (67% target likelihood), low (33% target likelihood), and neutral (50% chance of target presence or absence). **B** Traveling waves were assessed across 8 lines of electrodes positioned along the anterior-posterior axis in the prestimulus period (−600 ms to 0 ms). These electrode lines were either contralateral or ipsilateral to the stimulus location. **C** Violin plots show the distribution of sensitivity (d′) and **D** criterion (c) across conditions (Supplementary Data 1). Dots represent individual participants. Vertical bars indicate the interquartile range (25th–75th percentiles). Prior information did not affect sensitivity ($F_{2,158} = 1.22$; $p = 0.30$, ηp2 = 0.01) but had a substantial influence on decision strategies ($F_{2,158} = 89.04$; $p < 0.01$, ηp2 = 0.53). Specifically, participants adopted a more conservative criterion when the cue indicated a low probability of the target ($c_{\text{low probability}} = 0.63 \pm 0.05$), compared to trials with a neutral cue ($c_{\text{mid probability}} = 0.37 \pm 0.05$; $t_{79} = 7.15$, $p < 0.01$, BF > 1000) or a high probability cue ($c_{\text{high probability}} = -0.02 \pm 0.05$; $t_{79} = 9.87$, $p < 0.01$, BF > 1000). Moreover, a more liberal criterion was observed when the high probability cue preceded the checkerboard, relative to the neutral cue ($t_{79} = -9.78$, $p < 0.01$, BF > 1000).

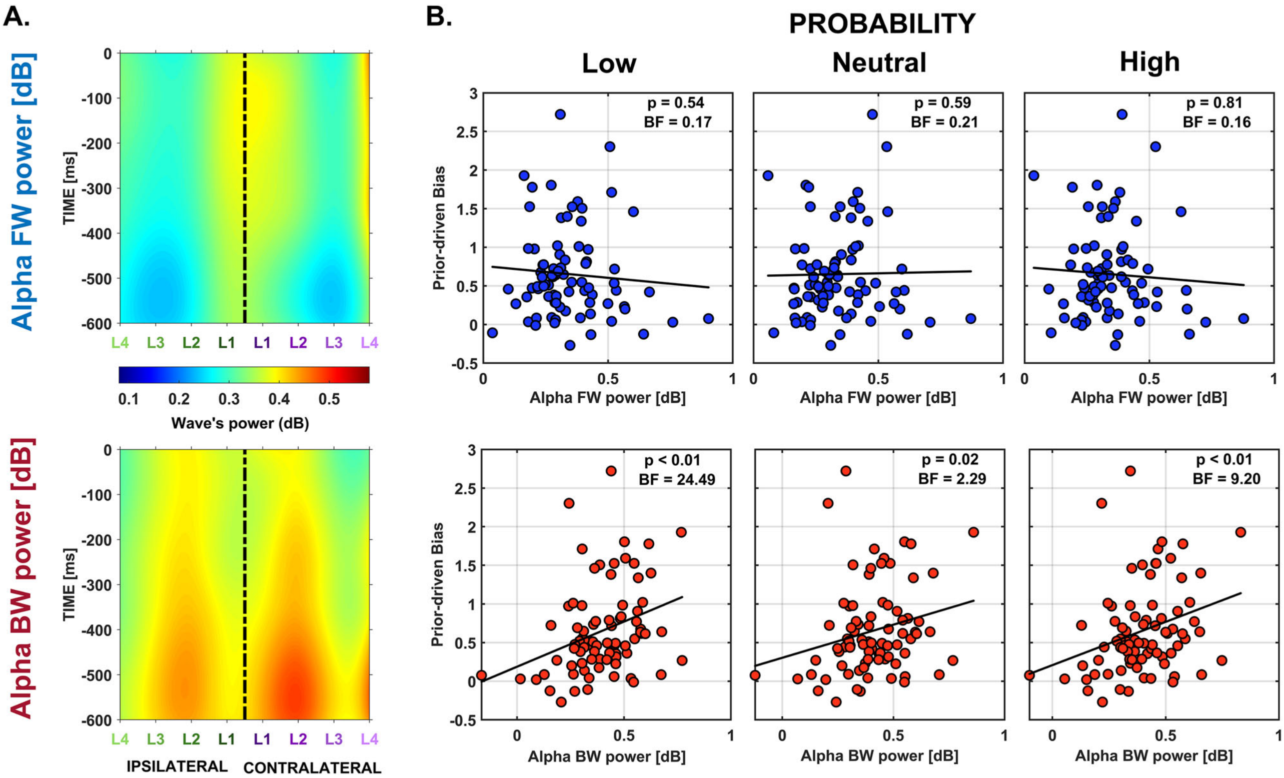

Fig. 2 | Influence of expectation-like information on traveling wave patterns. **A** We quantified the dynamics of backward and forward alpha band waves in both the contralateral (i.e., right) and ipsilateral (i.e., left) hemispheres relative to stimulus presentation. The time axis depicts the temporal evolution of prestimulus wave power from −600 to 0 ms relative to stimulus onset, showing how wave power dynamically changes throughout the prestimulus interval across different electrode lines (spatial dimension), with blue representing low power and red indicating high power. A lateralization effect is observable, showing a significant increase in contralateral backward waves in the alpha band. In contrast, forward waves are comparable between the two hemispheres. **B** Statistical analysis (Supplementary Data 2) revealed the presence of an interaction between cue (low, neutral, and high probability) and criterion modulation when considering the alpha BW waves in the contralateral hemisphere ($F_{2,156} = 4.95$, $p < 0.01$, ηp2 = 0.06). Specifically, prestimulus BW waves in both the low (Spearman = 0.35, $p < 0.01$, BF = 24.49) and high (Spearman = 0.32, $p < 0.01$, BF Kendall = 9.20) probability conditions significantly predicted the magnitude of decisional bias. A similar, though weaker, relationship was also observed in the neutral condition (Spearman = 0.26, $p = 0.02$, BF Kendall = 2.29). Notably, contralateral alpha band forward waves did not predict the degree of criterion modulation in any of the cues considered (all $p > 0.54$, all BF Kendall < 0.18). For visualization purposes, the figure presents the average alpha FW/BW for each subject across contralateral electrodes, as the effect was not specific to any individual electrode line.

indicate whether they detected the target. Initially, each participant completed an adaptive titration phase similar to the one employed in refs. 33–35 to determine the contrast level of the gray circles that would yield a detection accuracy of 70%. In the subsequent phase, the checkerboards were preceded by a symbolic cue that signaled the likelihood of the target's appearance. There were three levels of cue probability: a high probability cue indicated a 67% chance of target presence (high probability condition), a low probability cue indicated a 33% chance (low probability condition), and a neutral cue indicated an equal probability (50%) of target presence or absence. The actual target presentation adhered to these probabilities, and participants were explicitly informed that the cues reliably reflected the likelihood of the target's appearance. We computed the signal detection theory indices d' (sensitivity) and c (criterion) (Green and Swets, 1966) separately for trials preceded by low, high, or neutral probability cues. As demonstrated in the previous publications[20,32], the repeated-measures ANOVA revealed no significant effect of the probabilistic cue on *d'* (Fig. 1C; $F_{2,158} = 1.22$; $p = 0.30$, ηp2 = 0.01). However, the probabilistic cue significantly influenced the criterion (Fig. 1D; $F_{2,158} = 89.04$, $p < 0.01$, ηp2 = 0.53). Participants adopted a more conservative criterion when the cue indicated a low probability of the target ($c_{\text{low probability}} = 0.63 \pm 0.05$), compared to trials with a neutral cue ($c_{\text{mid probability}} = 0.37 \pm 0.05$; $t_{79} = 7.15$, $p < 0.01$, BF > 1000) or a high probability cue ($c_{\text{high probability}} = -0.02 \pm 0.05$; $t_{79} = 9.87$, $p < 0.01$, BF > 1000). Moreover, a more liberal criterion was observed when the high probability cue preceded the checkerboard, relative to the neutral cue ($t_{79} = -9.78$, $p < 0.01$, BF > 1000).

Backward traveling waves drive probabilistic cue integration in a perceptual decision-making task. We investigated how expectation-like information influences alpha band traveling wave patterns. First, we quantified the traveling waves' power (dB) in the contra- and ipsilateral hemispheres in the prestimulus period (−600 to 0 ms) (see Fig. 1B for electrode layout and extraction lines). We observed a lateralization effect revealing an increase of contralateral (vs ipsilateral) backward (but not forward) waves in the alpha band (Fig. 2A).

We statistically investigated whether the observed alpha band traveling wave pattern underpinned the integration of probabilistic cues in the perceptual task. To this end, we conducted two ANCOVAs, using CUE (low, neutral, high probability), LINE (1–4; distance from the midline), and HEMISPHERE (contralateral, ipsilateral) as factors, with CRITERION SHIFT—an index of cue integration (see "Methods")—included as a covariate. In the first ANCOVA, BW waves were included as the dependent variable, whereas in the second, FW waves served as the dependent variable.

The first ANCOVA focusing on alpha band backward waves (but not when considering theta or beta backward waves, Supplementary Tables S6–S13) revealed a significant three-way interaction among CRITERION SHIFT, HEMISPHERE, and CUE ($F_{2,156} = 4.95$, $p < 0.01$, ηp2 = 0.06). To further interpret this result, we examined the relationship between CUE and CRITERION SHIFT separately for each hemisphere. The analysis showed a significant CUE*CRITERION SHIFT interaction in the contralateral hemisphere ($F_{2,156} = 3.71$, $p = 0.03$, ηp2 = 0.05), whereas no significant effect was observed in the ipsilateral hemisphere ($F_{2,156} = 0.14$,

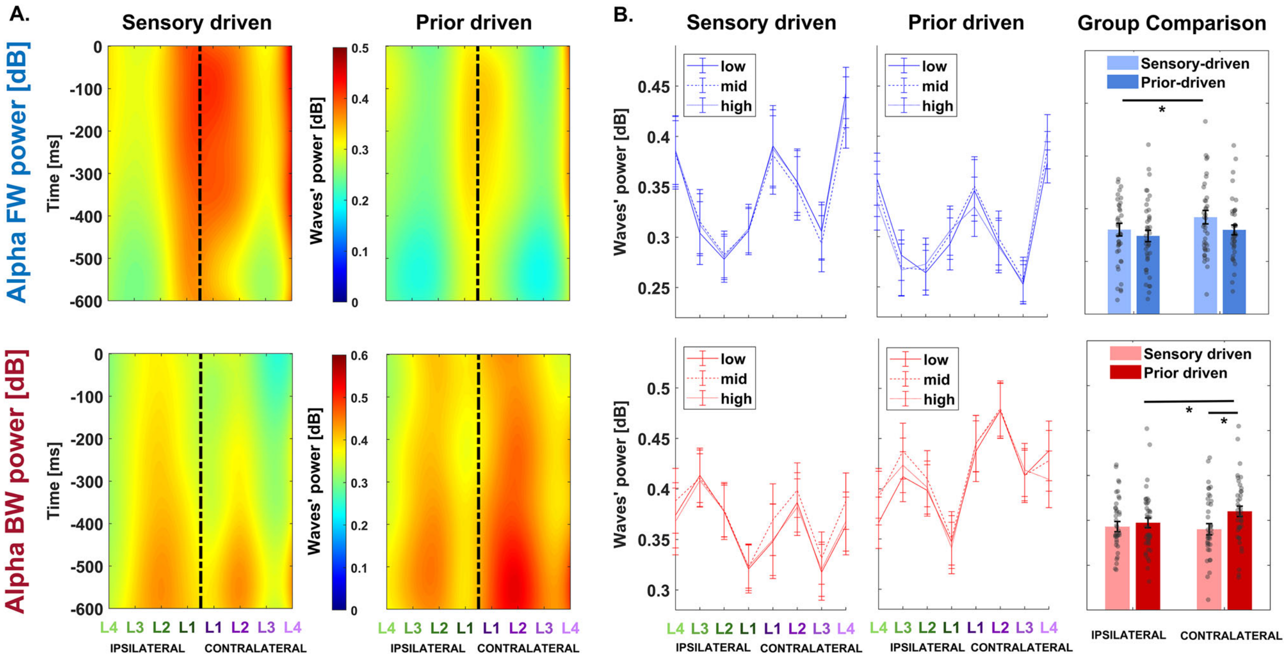

Fig. 3 | Patterns of traveling waves in prior-driven and sensory-driven individuals. **A** We computed forward and backward alpha band waves for individuals characterized by prior-driven ($N = 40$) vs sensory-driven decision-making ($N = 40$). The accompanying map depicts the power of these waves during the prestimulus period across the specified electrode lines, with bluish colors indicating low power and reddish colors representing high power. **B** We observed a hemispheric difference in the traveling waves' power (Supplementary Data 3) that was moderated by the group factor ($F_{2,156} = 3.54$, $p = 0.03$, ηp2 = 0.04). Specifically, sensory-driven individuals exhibited a higher prevalence of forward waves in the hemisphere contralateral to stimulus presentation compared to the ipsilateral one ($F_{1,39} = 8.29$, $p < 0.01$, ηp2 = 0.17). In contrast, prior-driven individuals demonstrated stronger backward waves in the contralateral hemisphere ($F_{1,39} = 11.52$, $p < 0.01$, ηp2 = 0.22), along with a higher overall BW waves' power compared to the sensory-driven group, particularly in the contralateral hemisphere (all $t < -1.99$, all $p < 0.05$, BF low probability = 3.24, BF mid probability = 1.28, BF high probability = 2.87). This spatial specificity is noteworthy, as the integration of expectations predominantly occurs during the pre-stimulus period in the hemisphere responsible for processing the stimulus. In this study, the right hemisphere played this role, given that the stimulus was consistently presented on the left. Dots represent individual participants. Vertical bars indicate the interquartile range (25th–75th percentiles).

$p = 0.87$, ηp2 < 0.01). Post-hoc analyses revealed that the prestimulus BW alpha waves extracted from the low probability (Pearson = 0.33, $p < 0.01$; Spearman = 0.35, $p < 0.01$; Kendall = 0.25, $p < 0.01$; skipped Pearson = 0.34, CI = [0.13, 0.53]; skipped Spearman = 0.35, CI = [0.12, 0.56], BF Pearson = 9.04, BF Kendall = 24.49) and high-probability conditions (Pearson = 0.30, $p < 0.01$; Spearman = 0.32, $p < 0.01$, Kendall = 0.22, $p < 0.01$; skipped Pearson = 0.34, CI = [0.14, 0.50]; skipped Spearman = 0.33, CI = [0.10, 0.52], BF Pearson = 4.85, BF Kendall = 9.20) significantly predicted the extent of criterion modulation (Fig. 2B). The association between BW in the neutral condition and criterion modulation also showed a significant association (Pearson = 0.23, $p = 0.04$; Spearman = 0.26, $p = 0.02$; skipped Pearson = 0.27, CI = [0.07, 0.48]; skipped Spearman = 0.28, CI = [0.06, 0.50], BF Pearson = 1.13, BF Kendall = 2.29). Conversely, in the second ANCOVA focused on prestimulus FW waves, we found no significant effect of the covariate CRITERION SHIFT nor any interaction with this covariate (all $F < 2.67$, all $p > 0.07$, all ηp2 < 0.03). To rule out potential confounds due to spatial leakage, we repeated these ANOVAs after applying a surface Laplacian to the EEG signal, obtaining the same pattern of results (see "SI").

These findings demonstrate that prestimulus alpha band backward traveling waves reflect a key neural mechanism supporting probabilistic cue integration, with a significant laterality effect driven by top–down activity in the contralateral hemisphere responsible for processing sensory input. This suggests that expectation-like cues modulate neural dynamics, effectively preparing the brain activity of the relevant hemisphere to incoming stimuli in the expected contralateral hemifield.

Interindividual differences in cue integration strategies are reflected in distinct traveling wave profiles. In our previous research[20], we identified two distinct groups based on their use of predictive information (see "Methods"). The prestimulus amplitude of the posterior alpha band oscillations allowed us to intercept these differentiations: participants who exhibited a greater suppression in the amplitude of alpha band oscillations in the high-probability vs low-probability condition showed a concurrent strong bias shift (prior-driven individuals), reflecting a more pronounced modulation of their criterion. In contrast, individuals who exhibited a reduced modulation of alpha band amplitude showed a dampened criterion shifting (sensory-driven individuals).

Here, we aimed to investigate whether traveling wave patterns could reveal the underlying processes driving individual differences in the integration of expectations during decision-making. To accomplish this, we extracted alpha FW and BW waves (Fig. 3A, B) from individuals exhibiting above-median cue-driven modulation of their alpha band amplitude oscillations (prior-driven group) and compared them to those in a group with lesser modulation (sensory-driven group). We hypothesized that the prior-driven group would exhibit stronger alpha band BW activity, whereas the sensory-driven group would display an opposite pattern, characterized by increased alpha FW activity. Importantly, we predicted that these effects would be present in the contralateral hemisphere relative to the stimulus position, compared to the ipsilateral hemisphere. Furthermore, we incorporated the different electrode lines used to extract the traveling waves in the analyses, aiming to investigate whether the hypothesized hemisphere effect was, in turn, modulated by the particular electrode line under examination.

The ANOVA, with BW alpha band waves as the dependent variable and within-subject factors HEMISPHERE (contralateral, ipsilateral), LINE (distance from the midline), and CUE (low, neutral, high probability), along with the between-subject factor GROUP (Prior-driven, Sensory-driven), revealed a significant interaction between HEMISPHERE, CUE, and GROUP ($F_{2,156} = 3.54$, $p = 0.03$, ηp2 = 0.04). Splitting the ANOVA by the GROUP factor revealed no significant effects in the sensory-driven group (all $F_{2,78} < 1.89$, all $p > 0.16$, all ηp2 <0.05). In contrast, the prior-driven group showed a significant main effect of HEMISPHERE ($F_{1,39} = 11.52$, $p < 0.01$, ηp2 = 0.22), indicating that alpha band BW waves were more prevalent in the hemisphere contralateral to stimulus presentation (mean alpha band BW contralateral = 0.44 ± 0.02 dB) compared to the ipsilateral hemisphere (mean alpha band BW ipsilateral = 0.39 ± 0.02 dB). The direct contrast of BW waves between the sensory-driven and prior-driven groups showed that, while both groups exhibited similar levels of BW alpha band waves in the ipsilateral hemisphere across all cue levels (all $t > -0.66$, all $p > 0.76$, all BF > 0.28), a significant difference emerged in the right hemisphere, with the prior-driven group showing a higher prevalence of BW waves (all $t < -1.99$, all $p < 0.05$, BF low probability = 3.24, BF mid probability = 1.28, BF high probability = 2.87). These post hoc results confirm our initial hypothesis, as the observed interaction and subsequent contrasts indicate that the effects of cue probability and group are modulated by hemisphere. Specifically, the contralateral hemisphere shows distinct patterns of BW alpha band activity depending on whether the participant adopted a prior-driven or a sensory-driven approach.

Our second hypothesis was partially confirmed, as we observed a trend-level interaction between HEMISPHERE, CUE, and GROUP when analyzing alpha band FW waves ($F_{2,156} = 2.63$, $p = 0.07$, ηp2 = 0.03). Although not statistically significant, this finding suggests that the effects of cue probability and hemisphere are modulated by the considered group, in line with our initial predictions. Indeed, further investigation of this interaction, split by the GROUP factor, revealed a pattern opposite to that observed in the BW waves analysis. Specifically, in the prior-driven group, no relationship between cue and hemisphere was found ($F_{2,78} = 0.80$, $p = 0.45$, ηp2 = 0.02). In contrast, a main effect of HEMISPHERE emerged in the sensory-driven group ($F_{1,39} = 8.29$, $p < 0.01$, ηp2 = 0.17), indicating that FW waves were more prominent in the hemisphere contralateral to stimulus presentation (mean FW contralateral = 0.37 ± 0.03 dB) compared to the ipsilateral hemisphere (mean FW ipsilateral = 0.32 ± 0.02 dB) in this group.

Finally, we investigated whether the two groups showed differences in theta and beta oscillations as a function of the other factors tested (see “SI”). For theta oscillations, the group factor did not show any significant differences, nor did it interact with the other factors, whether considering theta FW or BW waves (all $F < 2.68$, all $p > 0.07$, all ηp2 < 0.03). Crucially, a significant interaction between GROUP, LINE, and HEMISPHERE emerged when considering beta BW waves. Follow-up ANOVA, splitting by the GROUP factor, revealed a significant LINE * HEMISPHERE interaction for both the prior- and sensory-driven groups (all $F > 3.17$, all $p < 0.01$, all $\eta p^2 > 0.09$). To further investigate these significant results, we conducted independent *t*-tests to examine whether the two groups showed significant differences across the four lines as a function of the considered hemisphere. The analysis revealed a significant increase in the BW waves in the left hemisphere, ipsilateral to the presented stimulus hemifield, for the sensory-driven group across all the considered lines (all $t_{39} > 2.21$, all $p < 0.03$, all BF > 1.50), except for the line farthest from the midline ($t_{39} = 1.66$, $p = 0.10$, BF = 0.60). Conversely, the prior-driven group showed an opposite pattern, with stronger beta BW waves in the right hemisphere, contralateral to the presented stimulus hemifield, compared to the left in the two lines closer to the midline (all $t_{39} > 2.69$, all $p < 0.01$, all BF > 3.89), while no differences were observed in the more distant lines (all $t_{39} < 1.48$, all $p > 0.13$, all BF < 0.47). These effects closely resemble, albeit to a lesser strength, those observed within the alpha band.

Backward waves correlate with alpha band power modulation. In our previous publication, we demonstrated that the modulation of parieto-occipital alpha band amplitude underpins the integration of probabilistic cues into perceptual processing (Fig. 4A). Furthermore, Kloosterman et al. [21] showed that modulation of posterior alpha band amplitude strategically biases evidence accumulation during perceptual tasks. Building on this, we investigated whether the prior-driven effects observed in backward alpha band waves were linked to alpha band amplitude modulation. We found that contralateral alpha band backward traveling waves correlated with the modulation of parieto-occipital alpha band power (Fig. 4B; Pearson = 0.26, $p = 0.02$; Spearman = 0.28, $p = 0.01$; Kendall = 0.20, $p = 0.01$; skipped Pearson = 0.24, CI = [0.06, 0.41]; skipped Spearman = 0.27, CI = [0.08, 0.46], BF Pearson = 2.06, BF Kendall = 3.93). These results suggest that alpha band traveling waves are associated with enhanced modulation of alpha band amplitude. Importantly, this relationship was not significant when considering alpha band FW waves or BW waves extracted from the ipsilateral hemisphere (Fig. 4B; all $p > 0.74$). Moreover, we demonstrated a positive trial-by-trial relationship between contralateral backward traveling waves and alpha band amplitude (see “SI”), replicating the findings of Alamia et al. [11] that revealed the association between these two measures. To further investigate a potential connection between traveling waves, alpha band amplitude modulation, and decision criterion adjustments driven by prior cues, we established a mediation model to examine whether the relationship between backward alpha band waves and criterion modulation was mediated by concurrent changes in alpha band oscillation amplitude (Fig. 4C). Crucially, we found a significant mediation effect (Indirect effect = 0.25, CI = [0.06, 0.67]), where an increase in backward alpha band waves are associated with the modulation of decision criterion through a concurrent modulation of alpha band amplitude. The link between backward alpha waves, alpha power modulation, and criterion shifts also held after Laplacian filtering, confirming that the effect was not driven by spatial smearing (see “SI”). This suggests that backward alpha band waves play a key role in shaping decision-making processes by influencing the local alpha band power, which in turn affects how prior information is integrated into perceptual judgments.

Discussion

Previous studies have shown that presenting participants with cues about the likelihood of specific outcomes can significantly bias their decision-making processes. For example, when participants are informed that a target is more likely or unlikely to appear, their rate of reporting the target’s presence increases or decreases accordingly[5,10,20,32]. These findings demonstrate that cue-based expectations significantly impact perceptual judgments, underscoring the crucial role of prior information in shaping decision outcomes.

While low-frequency oscillations and their role in top–down signaling have been described previously[3,4,11,36,37], to our knowledge, this is the first study in healthy human participants to demonstrate that the propagation of prestimulus alpha band traveling waves is directly modulated by explicit probabilistic expectations. Prior work has shown correlations between alpha band power and expectation[20,38–40], and several studies have characterized the role of traveling waves in high-level cognitive processes[11,28,41,42]. However, our paradigm uniquely manipulates perceptual expectations on a trial-by-trial basis using probabilistic cues, enabling a direct test of the link between traveling waves and predictive inference. This design revealed two key findings: first, that alpha band traveling waves are modulated by probabilistic expectations; and second, that this modulation exhibits a lateralized pattern aligned with the task structure, which consistently presented stimuli in the left hemifield. While previous studies have reported wave lateralization in the context of spatial attention[11], our results demonstrate for the first time that a comparable lateralization emerges in response to a probabilistic—rather than spatial—prior. Finally, by integrating behavioral modeling of decision-criterion shifts, we show that traveling-wave dynamics functionally support the implementation of perceptual predictions.

To clarify the spatial and directional properties of this modulation, we examined the directionality and hemispheric distribution of alpha band waves. We found a significant increase in prestimulus backward alpha band waves in the contralateral hemisphere (i.e., right), corresponding to the spatial location of the stimulus (i.e., left). This suggests that these waves effectively transmit predictive information to the visual regions responsible for processing the upcoming stimulus. This result supports the predictive coding framework, indicating that the brain uses top–down signals to

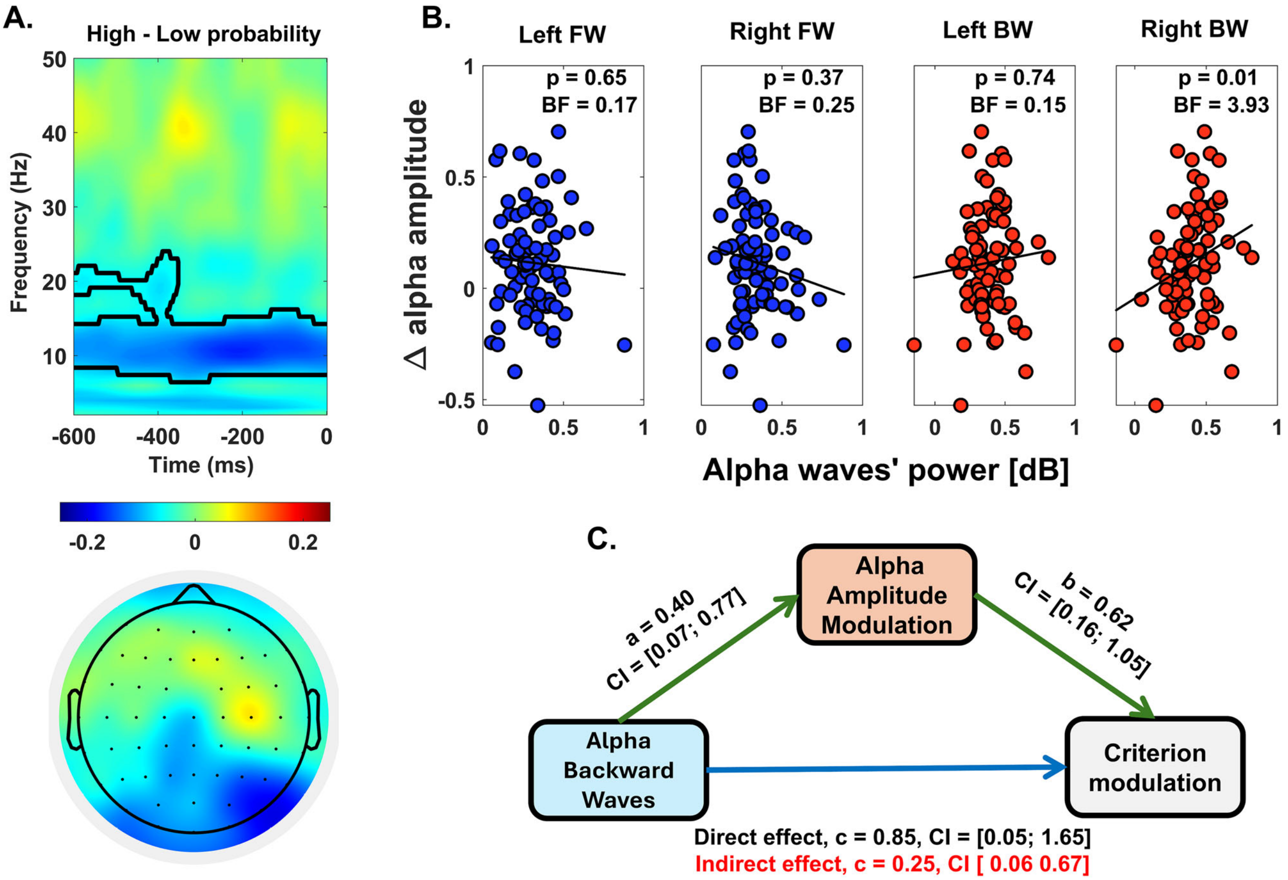

Fig. 4 | Backward alpha band waves modulate the amplitude of parieto-occipital alpha band oscillations. **A** The top panel shows the time-frequency map of the pre-stimulus period (−600 to 0 ms), highlighting the amplitude differences between high and low probability trials in regions associated with visual processing. Time 0 marks the onset of the stimulus, and black contours indicate statistically significant clusters. The bottom panel depicts the topographic distribution of alpha band activity differences between low and high probability conditions during the pre-stimulus window. The alpha band oscillatory activity diverges between conditions, specifically in the posterior electrodes ($p < 0.01$), with a pronounced peak in the right hemisphere. In contrast, the rest of the brain shows comparable activation levels. This highlights a spatially localized effect that modulates cortical activity in areas specialized for stimulus detection. **B** While the FW alpha band waves and BW waves recorded in the ipsilateral hemisphere did not have a significant effect on the modulation of alpha band oscillations (all $p > 0.36$, all BF < 0.26), the BW alpha band waves recorded in the right hemisphere significantly influenced the alpha band amplitude ($p = 0.01$, BF = 3.93). Specifically, the higher the BW alpha band waves, the greater the participant's ability to modulate the alpha band amplitude in the high vs low probability conditions. **C** The mediation analysis (Supplementary Data 4) demonstrates that traveling waves, alpha band amplitude, and decision bias modulation are interrelated. As shown in ref. 20, the degree of modulation of alpha band amplitude correlates with the magnitude of decision bias ($b = 0.62$, CI = [0.16; 1.05]). Similarly, the analyses conducted in this work revealed a significant relationship between the BW waves' power and the extent of induced bias. Crucially, we show here that the effect linking BW waves and decision bias is mediated by a concurrent modulation of alpha band oscillation amplitude [Mediation effect = 0.25, CI = [0.06; 0.67]). In other words, higher BW waves' power is associated with a greater proclivity to modulate alpha band amplitude, which, in turn, leads to a more pronounced decision bias.

prepare for anticipated sensory inputs. Moreover, they align with computational models proposing that alpha band oscillations serve as the neural code for implementing predictive inference in humans[43]. This relationship is further supported by the robust correlation observed between backward alpha band waves and prior-driven behavioral modulation in the task: participants exhibiting stronger backward-traveling alpha band waves were more likely to adjust their decision criteria according to the probabilistic cues. This highlights the dynamic nature of the alpha rhythm, actively contributing to the integration of expectation-like information into perceptual judgments. In contrast, our results showed no significant correlation between forward alpha band waves and prior integration. The absence of an association underscores a functional distinction between the roles of directional alpha band waves. Specifically, while backward-traveling waves seem essential for integrating predictive information, forward-traveling waves may serve different functions—likely related to the transmission of processed information through cortical hierarchies, rather than the integration of prior expectations. This result aligns with Alamia et al. [11], who demonstrated two functionally distinct traveling waves within the alpha band, propagating in opposite directions during an attentional task: backward waves, which dominate during top–down processes related to attention allocation, and forward waves, which are associated with real-time visual processing during stimulus presentation.

Interpreting traveling waves in scalp recordings presents substantial challenges, particularly when using non-invasive techniques such as MEG or EEG. For instance, prior research has demonstrated that locally confined waves at the mesoscale (e.g., within primary visual cortex, V1) can give rise to apparent large-scale traveling wave patterns at the macroscopic level in the sensor space[26]. Moreover, a recent theoretical study has indicated that phase-based analytical approaches may not necessarily reflect the genuine neural information flow[44], calling for caution when interpreting these results. Similarly, a previous study has shown that a single or pair of dipolar sources can reproduce scalp voltage patterns resembling traveling waves propagating in a forward (i.e., occipital to frontal) direction[45]. Although such a configuration of dipoles could, in theory, generate a wave-like pattern, and the waves we observed at the sensor level may be more localized in the source space, it would be unlikely to show a functionally relevant phase gradient in both directions modulated by cue predictability. However, our results are compatible with both accounts: either a wave propagating in a portion of the cortex, or a set of dipoles located in occipital and parietal regions. Further studies with invasive recordings may shed light on the source of the observed activity.

Additionally, we observed a significant correlation between backward waves and modulation of alpha band power in the parieto-occipital region, consistent with the findings of Kasten et al.[46] and Alamia et al.[11]. Our results support the hypothesis that top–down processes, as reflected by backward waves, drive the established relationship between alpha band power and prior information integration, as documented in the literature[20,21,38,40,47,48]. Crucially, mediation analysis corroborated this hypothesis, showing that the increase in the power of backward alpha band waves modulates the decision criterion through a concurrent modulation of alpha band amplitude. This suggests a hierarchical process in which the antero-posterior traveling waves, likely reflecting long-range communication of predictive information, modulate the local marker—posterior alpha band power—that underlies the integration of prior information. Ultimately, this hierarchically organized mechanism shapes behavioral outcomes that are sensitive to prior cues, as reflected in the modulation of the decision criterion during the task.

The observed increase in backward traveling waves likely reflects a preparatory mechanism that organizes cortical dynamics before the arrival of sensory evidence. Their prestimulus timing suggests that these waves contribute to establishing an anticipatory state, facilitating the integration of probabilistic cues into the upcoming perceptual process. Within predictive-coding frameworks, such backward alpha band propagation can be viewed as the large-scale transmission of top–down expectations that shape how sensory information is processed.

Moreover, prestimulus traveling waves within the alpha band accounted for the differences in predictive styles. Participants were classified in a data-driven manner based on the degree of prestimulus alpha band power modulation elicited by the probabilistic cue, a neural marker previously shown to index the integration of prior information[20], thereby distinguishing prior-driven individuals (*believers*) from sensory-driven individuals (*empiricists*). We found that only prior-driven participants, those who heavily integrate the cue into the decision-making process, exhibited an increase in backward-traveling waves. In contrast, sensory-driven participants, who rely more on sensory processing for their choices, showed a reduced presence of backward waves and an increased prevalence of forward waves. This weaker anterior-to-posterior flow suggests that sensory-driven individuals may minimally integrate the prior, as the functional pathway for this integration is under-exploited. In contrast, we observed an increased prevalence of forward-traveling waves in this group, which likely reflects a stronger reliance on sensory processing, where the brain prioritizes the transmission of processed sensory information rather than incorporating predictive cues. In line with previous findings, this pattern would not indicate a fundamental deficit but rather a distinctive integrative style, potentially linked to an autistic-like decision-making approach[32], which favors direct stimulus analysis over integrating prior information.

One interesting aspect of our findings is the lateralization of the effects. Specifically, only traveling waves flowing within the right hemisphere exhibited an increase compared to forward waves. Similarly, the increase in backward waves observed in prior-driven vs sensory-driven individuals was specifically found in the right hemisphere. This pattern emerged due to the consistent presentation of stimuli in the left visual field. Consequently, the increase in backward alpha band activity in the right hemisphere suggests that the brain fine-tunes prior integration by selectively modulating cortical areas involved in processing the target stimuli. This indicates a process carried out with high spatial specificity.

This specificity was intentionally reinforced in the design by holding target location constant in the left hemifield, ensuring stable spatial expectations and isolating cue-driven backward propagation. However, because the experiment did not include right-hemifield trials, it remains an open question whether the same modulation would shift to the opposite hemisphere when the expected location is reversed. Addressing this question will require future studies with block-wise manipulation of the stimulus hemifield.

We also investigated whether the observed effect was specific to alpha band oscillations or extended to other frequency bands. No significant differences were observed between the prior-driven and sensory-driven groups for FW and BW theta or FW beta waves. However, a difference emerged when examining BW beta waves: the prior-driven group exhibited increased beta activity in the contralateral hemisphere. This finding aligns with evidence suggesting that beta oscillations work in coordination with the alpha band to support the top–down transmission of predictive information[3,4,49].

This work can be expanded through various follow-up studies. For instance, individual differences in the power of these waves could be further investigated, particularly in the context of psychopathological conditions that may exacerbate these mechanisms. Notably, the strong emphasis on priors and idiosyncratic beliefs observed within the schizophrenic spectrum[50–53] may be linked to an increased transmission of backward alpha band waves[54,55]. This connection is particularly compelling in light of a recent study[56], which found that schizophrenia patients exhibited a substantial increase in top–down alpha band traveling waves and a decrease in bottom-up waves compared to healthy participants at rest. Investigating this population in tasks similar to the one employed in our study—where high-level explicit priors are provided—could serve as a benchmark for exploring the oscillatory underpinnings of predictive coding disruptions in schizophrenia. An excessive reliance on backward alpha band waves might indicate an over-integration of priors, potentially marking a distinct neural signature of this condition.

Moreover, an intriguing avenue for future research could involve establishing an information-based protocol designed to strengthen communication within the anterior-posterior networks through cortico-cortical paired-associative stimulation (ccPAS)[57–62]. ccPAS is a NIBS protocol that leverages Hebbian principles to enhance communication efficiency between networks[63]. This is achieved by repeatedly pairing TMS pulses delivered to specific nodes within the network at precise, network-dependent timings. By tailoring the timing between the two TMS pulses, it would be possible to achieve modulation in cortical connectivity specific to the frequency of interest (e.g., 100 ms to strengthen alpha band wave propagation)[59,61]. Targeting the anterior-to-posterior networks involved in conveying predictive activity with this specified timing may facilitate the causal modulation of alpha band traveling waves along the predictive chain, thereby enabling an investigation into their causal role in predictive coding.

In conclusion, our study underscores the crucial and frequency-specific role of backward traveling alpha band waves in the integration of prior information during perceptual decision-making. By delineating the mechanisms through which expectation-like signals influence perceptual processes, we have contributed to understanding the underlying codes upon which the brain's predictive processing relies.

Methods

Participants

Eighty healthy participants drawn from the general population (43 female; age range 18–35) provided written informed consent before participating in the study. The study was conducted in accordance with the Declaration of Helsinki and received approval from the Bioethics Committee of the University of Bologna (protocol code 201723, approved on August 26, 2021). The sample is drawn from a previously published dataset[32]. All ethical regulations relevant to human research participants were followed.

Stimuli and experimental design

Stimuli were presented on an 18-inch CRT display (resolution 1280 × 1024 pixels, refresh rate 85 Hz) positioned 57 cm away in a dimly lit room. Participants sat comfortably in front of the monitor. The stimuli were generated and displayed using Matlab (version 2016, The MathWorks Inc., Natick, MA) and the Psychophysics Toolbox. The visual stimuli consisted of checkerboards appearing in the lower left visual field, which could either contain gray circles within the cells (target) or not (catch trials). Participants were instructed to indicate the presence (by pressing key 'k' with the middle finger) or absence (by pressing key ‘m’ with the index finger) of the gray circles inside the checkerboard as quickly and accurately as possible. To avoid confounding effects related to motor programming, participants responded with their right hand, as this would engage the hemisphere opposite (i.e., the left) to the one responsible for sensory processing in the task (i.e., the right). The study was divided into two phases. In the first, each participant underwent an adaptive titration procedure to determine the contrast of the gray circles for which the detection accuracy was at ~ 70% when an equal number of target-present and target-absent trials (catch trials) was presented (For a detailed explanation of the titration procedure, see ref. 33. The second phase comprised 6 blocks of 90 trials each. Each trial started with the appearance of the probability cue presented at the center of the screen. The cue was presented for 1 s, followed by a fixation dot. After a variable delay of 1.2–1.5 s, a checkerboard containing (or not) gray circles at the titrated contrast within it appeared at the bottom left of the monitor for 60 ms. We opted to present the stimulus in only one hemifield to prevent spontaneous fluctuations in attention between the two hemifields in the prestimulus period from interfering with the results. Participants had to determine the presence or absence of the gray circles within the checkerboard and press the button associated with their choice. No timeout has been set for the response. After collecting the response, the screen appeared black for 1.9–2.4 s in the inter-trial interval. The cue was a rectangle with its bottom colored in red and its top colored in blue. The percentage of the red shading to the entire rectangle indicated the probability that the checkerboard contained the gray circles (target) within it. There were three levels of cues. Cue high and cue low (informative cues) indicated the probability of the presence of the target of 67% and 33%, respectively. Instead, the neutral cue (uninformative cue) equally predicted (50%) the presence and absence of the target. The actual probability of target presentation was in accordance with the probability indicated by the cue. Participants were also explicitly told that the probabilistic cue was congruent with the actual probability of stimulus presentation.

Signal-detection theory (SDT) modeling

To assess participants’ performance, we applied SDT to compute two key measures: d’ and c[64]. *d’* represents stimulus sensitivity, with higher values indicating greater sensitivity to the stimulus. *c* represents the decision criterion, where values differing from 0 suggest a bias in decision-making. To determine the influence of probabilistic cues on sensitivity and decision criteria, we computed d’ and c separately for trials that followed low, high, and neutral probability cues.

These measures were calculated based on the proportion of hits (i.e., reporting target present in target-present trials) and false alarms (i.e., reporting target present in catch trials) using these formulas:

$$d' = Z(Hit\ Rate) - Z(False\ Alarm\ Rate)$$

$$c = -\frac{Z(Hit\ Rate) + Z(False\ Alarm\ Rate)}{2}$$

where $Z(x)$ represents the z-score transformation (the inverse function of the standard normal cumulative distribution). We conducted a repeated-measures ANOVA to examine the effect of cue type on sensitivity and decision criteria, with cue type (high, low, and neutral) as the within-subjects factor. To further interpret the results from the ANOVA, we performed post-hoc analyses using paired sample t-tests. Subsequently, for each individual, we calculated the difference in the criterion adopted between low- and high-probability trials (Δ criterion = $\text{criterion}_{\text{low probability trials}} - \text{criterion}_{\text{high probability trials}}$) as a measure of cue integration. A larger shift in the Δ criterion indicated a greater perceptual adjustment in response to the predictive cue. Conversely, a Δ criterion close to zero suggests minimal perceptual adjustment, indicating that the participant’s decision-making criteria remained stable regardless of the cue provided. In addition, we report in Supplementary Table S1 the same analyses performed on hit rate and false-alarm rate separately. Both measures increased as a function of cue probability, confirming that the cue manipulation systematically biased target-present reports and reproducing the same qualitative pattern captured by criterion shifts. All statistical analysis was conducted using the JASP software[65], including both frequentist analyses and Bayesian analyses performed using the default prior settings provided by JASP.

EEG analysis

Participants sat comfortably in a dimly lit room. EEG data were collected using a 64-electrode cap, following the international 10–10 system, with signals sampled at 1000 Hz and impedances kept below 10 kΩ. EEG processing was performed offline using MATLAB scripts (version R2021a) and the EEGLAB toolbox[66]. The EEG recordings were filtered in the 0.5–100 Hz range using EEGLAB’s pop_eegfiltnew function with default parameters, and a 50 Hz notch filter was applied. The EEG signals were visually inspected, and any noisy channels were spherically interpolated ($M = 4.34 \pm 0.7$). Epochs from −4100 to 2000 ms relative to the checkerboard onset were extracted. After artifact rejection, participants contributed on average 463.8 ± 7.7 clean epochs to the final analyses. The recordings were then re-referenced to the average of all electrodes, and independent component analysis (ICA) was applied to remove artifacts distinguishable from brain-driven EEG signals ($M = 4.5 \pm 1.4$). After artifact removal, the signals were downsampled to 256 Hz.

Traveling wave analysis

We applied a method comparable to that of Alamia et al. [11] and Pang et al. [31] to assess the propagation of traveling waves across eight lines of seven electrodes, extending from the occipital to frontal regions. As depicted in Fig. 1B, we analyzed four lines distributed across the left (ipsilateral) and right (contralateral) hemispheres, symmetrically aligned with the midline. The electrode selection overlapped to cover a substantial portion of each hemisphere. For each group of seven electrodes, we generated 2D maps by sliding a 500-ms time window across the EEG signals, with a 125-ms overlap, and computed the 2D-FFT for each map (Fig. 5). Importantly, the spectrum of the 2D-FFT transformation provides information about the phase shift in the signals of the seven electrodes. In particular, the 2D-FFT power in the lower and upper quadrants quantifies the waves propagating in the forward (FW—from occipital to frontal electrodes) and backward (BW—from frontal to occipital) directions, respectively. However, the 2D-FFT transformation combines both the spatial component (i.e., the phase shift in the signal, that is, the traveling waves component) and the temporal one (i.e., the $1/f$ and the oscillatory dynamics present in each signal separately, unrelated to the propagation through electrodes). To isolate the spatial component, we then computed a baseline measure by repeating the same process after having shuffled the electrodes’ position, in order to remove the spatial component from the baseline, while preserving the temporal information. Finally, the measure used to quantify the waves was obtained by comparing the ordered and the shuffled data via a log-ratio, for all frequencies between 2 and 45 Hz. More specifically, as in previous studies[11,67], we divided the maximum values in the 2D-FFT spectra for the actual (FW and BW) data with the shuffled data (FWss and BWss), yielding the wave power in decibels [dB]:

$$\text{FWdb} = 10 * \log 10 \frac{\text{FW}}{\text{FWss}} \quad \text{BWdb} = 10 * \log 10 \frac{\text{BW}}{\text{BWss}}$$

Importantly, this analysis was applied separately to each line of electrodes, and for each trial.

Finally, we conducted two ANCOVAs, one for each wave direction (forward and backward waves), to evaluate the role of traveling waves in integrating prior information. All traveling wave analyses were conducted by averaging the wave’s power over the prestimulus interval (−600 to 0 ms relative to stimulus onset). The analyses included the factors HEMISPHERE (ipsilateral; contralateral), LINE (1–4, representing the distance from the midline), and CUE (low, neutral, and high probability cue), with Δ

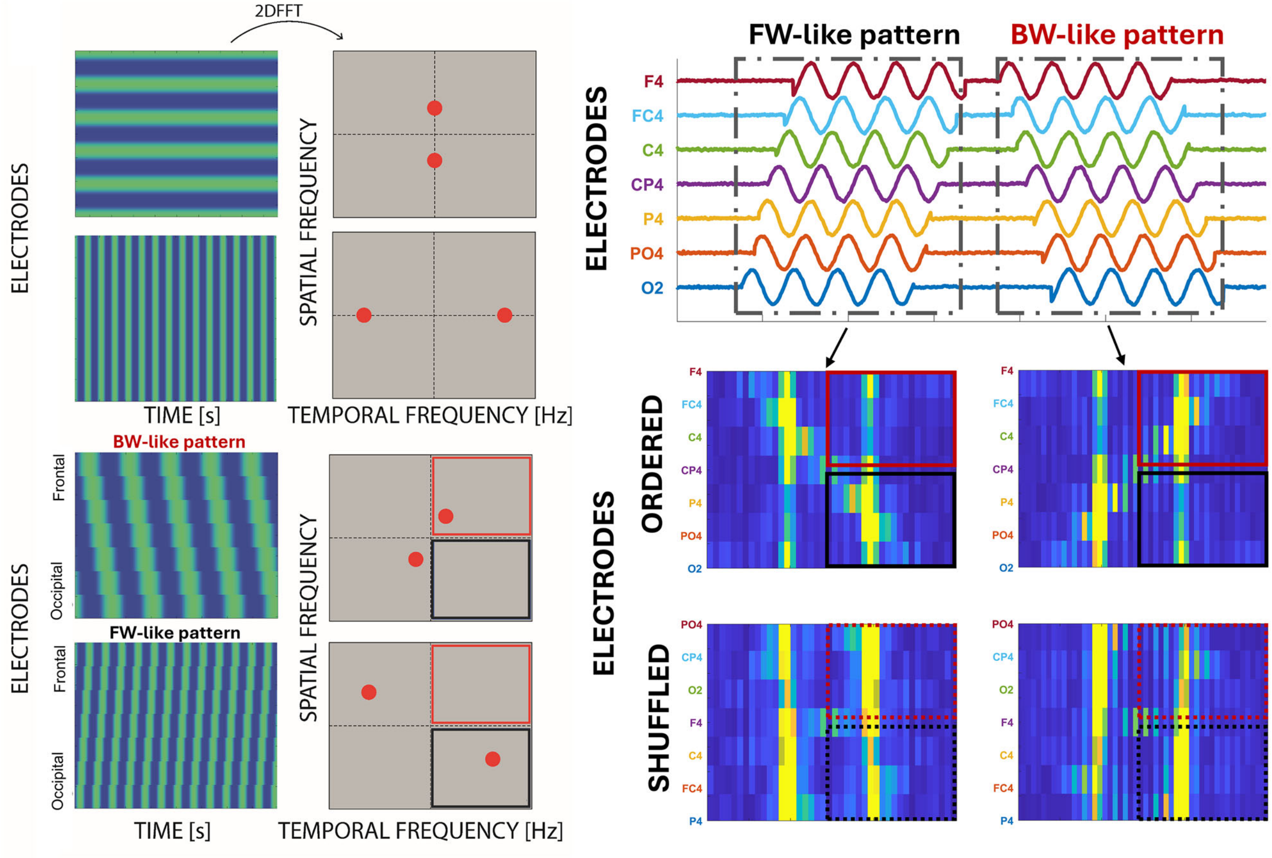

Fig. 5 | Waves analysis. To quantify the direction of traveling waves, prestimulus (−600 to 0 ms) EEG signals were arranged as space × time maps by stacking seven electrodes aligned along the occipital–frontal axis, and a 2D Fast Fourier Transform (2D-FFT) was computed on sliding 500-ms windows (step: 125 ms). In the resulting 2D spectrum, the horizontal axis represents temporal frequency, whereas the vertical axis represents spatial frequency, reflecting the phase gradient across electrodes. Because waves traveling from occipital to frontal sites (forward, FW) and from frontal to occipital sites (backward, BW) project onto opposite quadrants of the 2D-FFT, the maximum power in the lower and upper quadrants provides a directional estimate of propagation. To dissociate true spatial propagation from non-spatial spectral structure (e.g., $1/f$ and local oscillatory pattern), the same analysis was repeated after randomly shuffling electrode order within each line, which preserves temporal dynamics but removes spatial phase structure. Directional wave strength was then computed as a log-ratio between the ordered (FW, BW) and shuffled (FW_{ss}, BW_{ss}) spectra for each frequency between 2 and 45 Hz. This procedure was applied independently to each electrode line. Finally, FW and BW wave power was averaged within the theta (5–7 Hz), alpha (8–14 Hz), and beta (15–30 Hz) bands to obtain frequency-specific traveling-wave indices for statistical comparison across conditions.

CRITERION as a covariate (Supplementary Tables 2 and 3). The inclusion of the HEMISPHERE factor was essential, as we hypothesized that the effect of traveling waves in prior integration would be specific to the contralateral hemisphere relative to the stimulus presentation. Additionally, the LINE factor was incorporated to explore whether, within each hemisphere, the position along the medial-lateral axis influenced the observed effects. In these ANCOVAs, we focused exclusively on significant effects involving the covariate Δ CRITERION. This choice was driven by the primary aim of the study: to determine how traveling waves contribute to the utilization of perceptual priors and how this process is modulated by cue type, hemisphere, and electrode line position. Any relationships that did not interact with Δ CRITERION were deemed outside the scope of this investigation. We also performed the same analyses on waves extracted from the theta band (5–8 Hz) and beta band (15–25 Hz) to assess the frequency specificity of the effect mediated by the waves in the use of prior information. All ANCOVA results are presented in the supplementary tables.

Traveling waves and interindividual differences

In our previous publication, we demonstrated that prestimulus (−600 to 0 ms) alpha band amplitude is a sensitive marker for interindividual differences in the weighting of expectations[20]. Specifically, we found that a strong modulation of parieto-occipital alpha band amplitude between high and low probability conditions was associated with individuals who adopted a prior-driven decision-making strategy. In contrast, individuals who employed a stimulus-oriented approach exhibited no such modulation. Specifically, individuals exhibiting higher alpha band power modulation were associated with a prior-driven profile, characterized by a greater criterion shift, while those with lower alpha band power modulation were linked to a sensory evidence-driven approach, marked by a reduced criterion shift (see refs. 20,32 for further details). This measure captures the relative modulation of alpha band power as a function of cue probability, rather than absolute amplitude differences. To examine whether these interindividual differences in prior-driven processing were reflected in traveling wave dynamics, we divided participants into two groups using a median split based on their alpha band power modulation index (following the same grouping procedure as in refs. 20,32). Participants with alpha band modulation values above the median were classified as the “prior-driven” group, while those below the median were classified as the “stimulus-driven” group. The dependent variable in the subsequent analyses was traveling wave power, which quantifies a fundamentally different property of neural oscillations than the spectral power modulation used for group assignment. Based on the group differentiation identified in previous studies, we conducted two additional ANOVA (one for each direction, FW and BW), with HEMISPHERE (ipsilateral or contralateral), LINE (1–4, representing the distance from the midline), CUE (low, neutral, and high probability cue), and GROUP (prior-driven vs sensory-driven) as factors (Supplementary

Tables 4 and 5). Similar to the approach used in the analyses involving criterion shift, we focused exclusively on effects that demonstrated a significant relationship with the GROUP factor or a significant interaction involving this factor. All other effects were deemed irrelevant to the objectives of the present study, as they did not directly contribute to understanding the role of the adopted predictive strategy in the processing of perceptual priors. To evaluate the frequency specificity of the effects mediated by the waves on the use of prior information, we performed the same analyses on waves extracted from the theta band and the beta band. All ANOVA results are presented in the supplementary tables.

Backward waves and alpha band power modulation

We investigated the relationship between prior-driven effects observed in backward alpha band waves and alpha band amplitude modulation by conducting Pearson and Spearman correlation analyses, along with their respective skipped versions[68], between backward alpha band waves and alpha band amplitude modulation. Furthermore, to more comprehensively assess the evidence in favor of the association hypothesis between backward alpha band waves and alpha band amplitude modulation, we also calculated Bayes Factors (BF_{10}) for both the Pearson correlation and Kendall's τ correlation. According to conventional criteria[69], $BF_{10} < 1/3$ indicates moderate evidence for the null, 1/3–3 is considered inconclusive, $BF_{10} > 3$ indicates moderate evidence, $BF_{10} > 10$ strong evidence, and $BF_{10} > 30$ very strong evidence in favor of the tested hypothesis. We also ensured that the same relationship did not hold when considering FW alpha waves or BW alpha waves recorded in the left hemisphere. Finally, we performed a mediation analysis to explore whether backward alpha band traveling waves influenced criterion shifts, with any effects on alpha band amplitude modulation serving as a mediator. We report 95% confidence intervals (CI) based on 1000 bootstrap iterations (bias-corrected). Statistical significance was tested by assessing whether 95% of the values excluded zero, as is typically done in this type of analysis[70].

Furthermore, we investigated whether there was a significant relationship between alpha band traveling waves and alpha band amplitude at the single-trial level (Supplementary Fig. S1). This analysis was motivated by previous findings suggesting a crucial link between these two indices[11]. To this end, we extracted the prestimulus power of backward alpha band waves at the single-trial level for each electrode line of the contralateral hemisphere. We then computed the average power by collapsing across the contralateral electrode lines. Next, we extracted the alpha amplitude again at the single-trial level. For each participant, we correlated the alpha amplitude with the BW waves' power. Finally, we performed a one-sample *t*-test against zero on the correlation coefficients to assess whether a significant group-level association existed between the two measures.

Statistics and reproducibility

All statistical analyses were performed using JASP and MATLAB. Analyses were conducted on biologically independent samples, defined as individual participants. Data from technical repetitions were first aggregated at the single-participant level and were not treated as independent observations. Sample sizes correspond to the number of participants contributing to each analysis and are reported in the previous section. Frequentist and Bayesian analyses were performed using default settings, and all preprocessing and analysis steps were applied uniformly across participants to ensure reproducibility.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data supporting the findings of this study are available in the Open Science Framework (OSF) repository at https://osf.io/qkgpb/files/osfstorage[71]. This includes the Supplementary Data used for all reported analyses.

Code availability

MATLAB code used for the traveling waves analysis in this study was adapted and extended from openly available code hosted at https://github.com/artipago/Travelling-waves-EEG-2.0

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Luca Tarasi: conceptualization, methodology, investigation, visualization, writing—original draft, and writing—review and editing. Andrea Alamia: methodology, visualization, supervision, writing—original draft, and writing—review and editing. Vincenzo Romei: conceptualization, supervision, writing—original draft, and writing—review and editing.

Competing interests

The authors declare that they have no financial competing interests or personal connections that could have potentially impacted the work presented in this paper.

Additional information

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