Prestimulus influences on auditory perception from sensory representations and decision processes

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The qualities of perception depend not only on the sensory inputs but also on the brain state before stimulus presentation. Although the collective evidence from neuroimaging studies for a relation between prestimulus state and perception is strong, the interpretation in the context of sensory computations or decision processes has remained difficult. In the auditory system, for example, previous studies have reported a wide range of effects in terms of the perceptually relevant frequency bands and state parameters (phase/power). To dissociate influences of state on earlier sensory representations and higher-level decision processes, we collected behavioral and EEG data in human participants performing two auditory discrimination tasks relying on distinct acoustic features. Using single-trial decoding, we quantified the relation between prestimulus activity, relevant sensory evidence, and choice in different task-relevant EEG components. Within auditory networks, we found that phase had no direct influence on choice, whereas power in task-specific frequency bands affected the encoding of sensory evidence. Within later-activated frontoparietal regions, theta and alpha phase had a direct influence on choice, without involving sensory evidence. These results delineate two consistent mechanisms by which prestimulus activity shapes perception. However, the timescales of the relevant neural activity depend on the specific brain regions engaged by the respective task.

perception | oscillatory brain activity | EEG | single-trial decoding | prestimulus effects

Sensory percepts depend not only on the environmental inputs but also on the internal brain state before stimulus presentation (1). Many studies have shown that the accuracy and speed of sensory performance change with the power and timing (phase) of rhythmic activity during a prestimulus period (2, 3). Studies in the auditory system, for example, have demonstrated that performance in detecting sounds and gaps in noise, or the discrimination of lexical stimuli, varies with the power and phase of rhythmic activity between about 1 and 12 Hz (4–9).

Although the collective evidence makes a strong case that prestimulus state shapes the processing and perceptual consequences of sensory inputs, the functional interpretation of these findings in the context of specific sensory computations or higher cognitive processes has remained difficult (7, 10, 11). Electrophysiological studies in animals have described the state dependency of firing rates relative to cortical oscillations (12–15). Hence, it is tempting to interpret the reported prestimulus effects in neuroimaging studies as direct evidence for a link between the neural gain of early sensory cortices and perception. However, this is difficult for two reasons. First, previous studies have used different behavioral protocols (detection and discrimination) and stimuli (tones in silence or noise, gaps in noise, or speech), and each has implied different frequency bands and state parameters as relevant (from 1 to 12 Hz, reporting effects for phase, power, or both). Second, given the coarse spatial resolution of neuroimaging, it has often been difficult to localize the observed correlation of prestimulus state with perception to a specific neural process or brain region. Hence, it remains unclear whether previously reported prestimulus influences indeed originate from auditory cortices, possibly reflecting changes in sensory gain, or result from other high-level regions that are involved in general decision making.

To disambiguate these two possibilities, we collected behavioral and EEG data during two auditory discrimination tasks relying on distinct acoustic features in the same participants. To dissect different stages of the sensory–perceptual cascade, we used single-trial decoding to separate earlier auditory from later decision-related activity (16–18). We then used linear modeling to quantify the relation between prestimulus activity, task-relevant sensory evidence, and perceptual choice within each of these components. This allowed us to directly quantify whether putative correlations of prestimulus activity with perceptual choice are mediated by an impact of prestimulus state on early auditory evidence, or arise from higher cognitive processes activated subsequent to early sensory representations.

Results

Behavioral Results. The discrimination tasks used here were modeled based on a previous target-in-background detection task that had revealed pretarget influences on perception similar to those reported in other auditory studies (4). Subjects performed frequency and intensity discrimination tasks on different days and judged which of two brief tones was higher in pitch (louder). Each tone lasted 50 ms (with a 50-ms delay) and the second tone was always the standard, whereas the first was higher or lower in pitch (or intensity) across seven levels of difficulty titrated around each participant's threshold (Fig. 1*A*). Targets were presented on a background cacophony created from the superposition of many naturalistic sounds (4). The complete sensory evidence necessary to perform the task (i.e., both target tones) was available 150 ms after target onset.

Group-level psychometric curves ($n = 13$ participants) are shown in Fig. 1*B*, and demonstrate the comparable performance across

Significance

The likelihood of perceiving a faint stimulus depends not only on the stimulus itself but also on the state of rhythmic brain activity preceding the stimulus. Previous neuroimaging results did not confirm this state dependency as arising from early sensory representations or later decision-related computations. We show that state affects perception via two mechanisms: one where the amplitude of slow-wave activity influences the scaling of early sensory evidence, and another where the time profile of the activity influences sensory decisions in areas governing cognitive processes. These findings reconcile the plethora of previous findings and delineate two relevant mechanisms.

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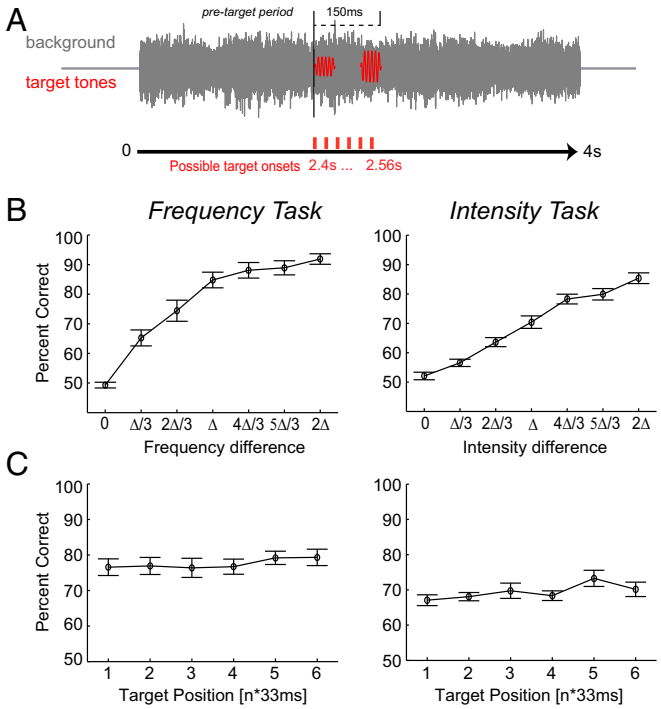

Fig. 1. Experimental paradigm and behavioral data. (*A*) Experimental paradigm. Target sounds (pure tones, each lasting 50 ms, 50-ms intertone interval) were presented at one of six possible time points ($2.4 + n*0.033$ s, $n = 0, \ldots, 5$) during a continuous acoustic background. The first tone varied in frequency (intensity) and was either increased or decreased by one of seven levels (titrated around each participant's psychometric threshold; Δ) relative to the second tone, which was the standard. (*B*) Group-level psychometric curves for each task, averaged across target positions (mean and SEM across participants; $n = 13$ participants). (*C*) Group-level performance (mean and SEM across participants) vs. target position, averaged across stimulus levels. There was no significant effect of target position (main text).

tasks [paired t test, $t(12) = 2.993$, $P = 0.096$]. The target tones were presented at six different time points relative to background to avoid expectancy effects (19, 20). There was no significant effect of target position on performance [frequency: ANOVA, $F_{(5, 72)} = 0.33$, $P = 0.892$; intensity: $F_{(5, 72)} = 1.41$, $P = 0.231$], suggesting that any dependency of perception on pretarget activity arises from neural processes not strictly entrained by the acoustic background (4, 5, 9).

Decoding Task-Relevant Sensory Evidence from EEG Activity. Using single-trial decoding applied across all stimulus levels, we searched for one-dimensional projections that maximally differed between the two conditions that participants were discriminating, namely which of the two tones was higher (in pitch or intensity). For both tasks, the decoding performance quantified by the receiver operator characteristic (ROC) was significant shortly after target presentation (randomization test, $P < 0.01$, corrected for multiple comparisons along time; Fig. 2*A*). We assessed the relevance of each projection for encoding task-relevant sensory evidence by computing neurometric curves for stimulus discrimination and neurobehavioral correlations (Fig. 2*B*). For both tasks, the neurobehavioral correlations were significant shortly after target presentation (randomization test, $P < 0.01$). Example neurometric curves are shown in Fig. 2*C*.

The scalp projections of the discriminating EEG components exhibited a systematic temporal pattern. Clustering projections in time revealed three distinct components for each task, which shared similarities between tasks. The average scalp projections and time epochs for each component are shown in Fig. 2*D*. The first component covered the time epoch during which the two target tones were being presented (up to t ~0.150 s). The second reflected typical auditory activations with central topographies (spanning 0.14–0.28 s for intensity and 0.13–0.28 s for frequency; termed the "auditory" component). For the intensity task this component was bilateral, whereas for the frequency task it was more right-lateralized, in agreement with the understanding that distinct auditory networks are involved in intensity and frequency judgments (21, 22). The third component comprised frontoparietal activations (spanning 0.28–0.4 s; termed "frontoparietal"), likely reflecting the transformation from auditory inputs to awareness (17, 23). The topography of this component differed between tasks

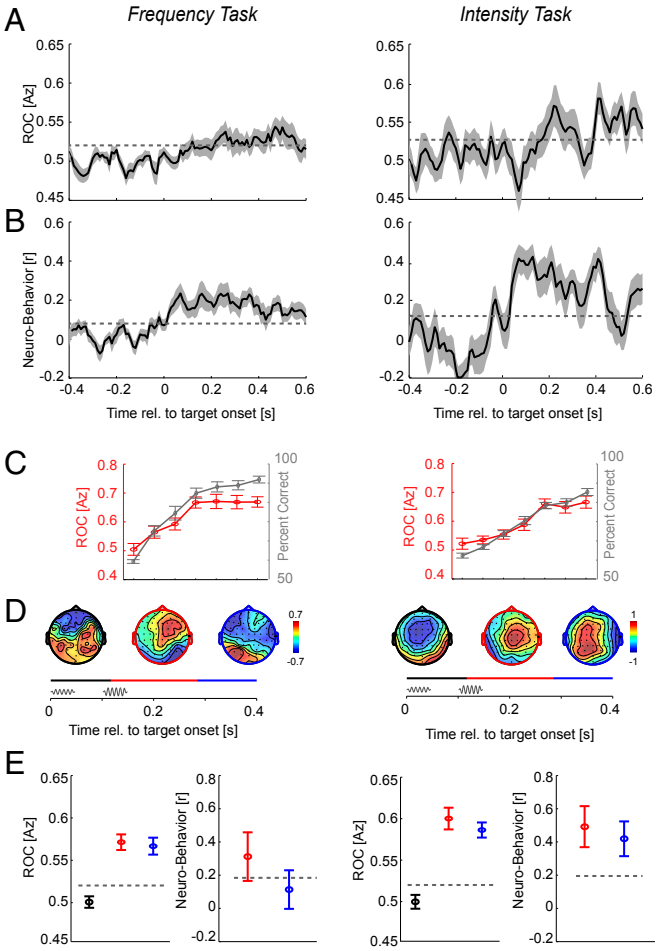

Fig. 2. Single-trial decoding of task-relevant evidence. (*A*) Performance of a linear classifier discriminating the two stimulus conditions (which tone was higher/lower) quantified using the ROC. Classification was performed using the EEG activity within 80-ms sliding windows (the time axis refers to the beginning of each window). Time is relative to target onset, and significance is relative to a randomization test (dashed lines; $P < 0.01$). (*B*) Correlation of psychometric curves with neurometric curves constructed from each classifier, with significance relative to a randomization test (dashed lines; $P < 0.01$). (*C*) Illustration of neurometric curves (derived from component 2, red, in *D*) together with the group-averaged psychometric curves (taken from Fig. 1). (*D*) *K*-means clustering the scalp projections of the classification components revealed three temporally continuous clusters that were consistent across participants and tasks. The first cluster spanned the period of target presentation (black), the second reflected early auditory activations (red), and the third reflected later frontoparietal activations (blue). (*E*) Stimulus discrimination performance and neurobehavioral correlations for each of the three components, with significance relative to a randomization test (dashed lines; $P < 0.01$). Lines and shaded areas as well as error bars show mean and SEM across participants ($n = 13$).

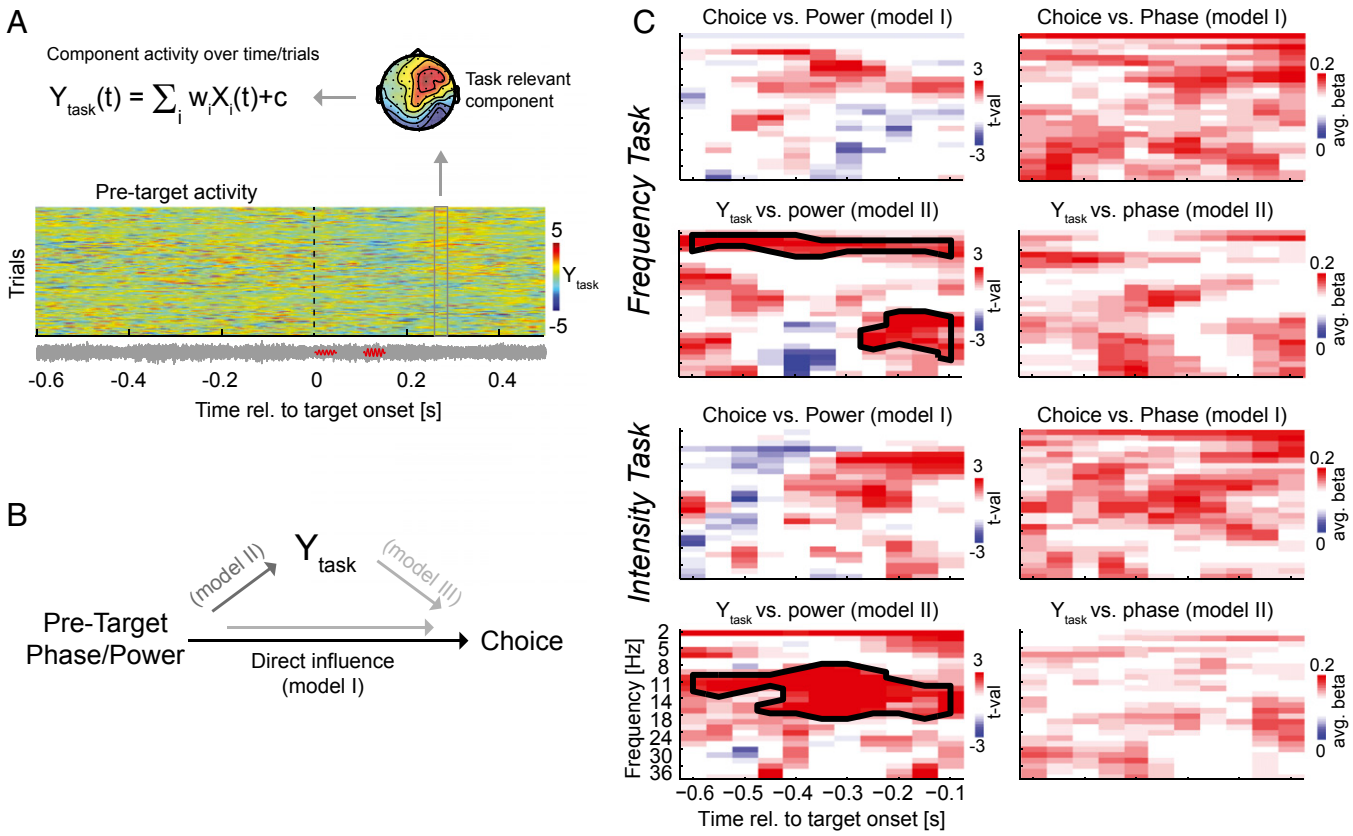

Fig. 3. Pretarget activity within auditory networks and relation to choice. (*A*) Single-trial activity within the auditory EEG component (cf. Fig. 2) was derived by projecting the data, $X(t)$, onto the respective subspace carrying the task-relevant information, $Y_{task}(t)$, separately for each participant, trial, and task. (*Lower*) Single-trial activity, $Y_{task}(t)$, for one participant across trials is displayed. The gray box indicates the time window at which the discriminating component was computed. (*B*) Possible pathways by which pretarget activity could influence perception. Model I tested for a direct influence of power/phase on choice without involving sensory evidence; model II tested for an influence of power/phase on sensory evidence (Y_{task}); model III tested for a combined effect of power/phase and evidence on choice. Comparing models II and III allowed testing for a mediation effect of state influences on choice through evidence, hence detecting statistical influences of pretarget activity on choice that are most likely explained by a putative influence on evidence. (*C*) Group-level regression statistics for both tasks and models I and II (showing group-level *t* values for power and group-level averages for phase). Significant time-frequency clusters are indicated in black (at $P < 0.05$, corrected for multiple comparisons across time-frequency bins, and FDR-corrected across regression models and tasks; $n = 13$ participants). The effect of sensory evidence on choice was significant for both tasks (main text). Within these auditory networks there was no direct effect of power or phase on choice.

in line with the notion that late frontoparietal EEG components reflect the heterogeneity of response strategies and latencies in sensory decision tasks (24). The between-subject similarities of each component did not differ between tasks [Fig. S1*A*; paired *t* tests, $t(12) = 1.7$, $P = 0.10$; $t = 1.3$, $P = 0.2$; and $t = 1.2$, $P = 0.22$, respectively]. The second and third components exhibited significant sensitivity to the stimulus condition in both tasks (ROC above 0.5; randomization test, $P < 0.01$), whereas the first component did not (Fig. 2*E*). Given that the first component did not capture significant task-relevant evidence and spanned a time period during which target presentation was not yet complete, we excluded this component from subsequent analysis. Neurobehavioral correlations were significant and strongest for the auditory component in both tasks, and for the frequency task they were significant only for this component (Fig. 2*E*).

Pretarget Influences in Auditory Networks. Having identified EEG components that characterize the networks carrying task-relevant sensory evidence allowed us to ask whether pretarget activity within these networks had a significant influence on perceptual choice. Hence, we exploited the low-dimensional projections defined by these classification components as windows onto specific neural processes involved in the sensory–perceptual transformation (16–18). Importantly, by extracting the component separately for each participant and task, we avoided the assumption of a common localization of effects across tasks or subjects, which has often been made in previous studies. Rather, we investigated prestimulus activity within the most relevant activity components for each participant and task. Based on previous studies, we expected to find an influence of pretarget activity on perception. However, it remained unclear whether these influences would be across tasks and whether they were mediated by sensory evidence reflected by the respective component.

Based on the weights associated with each component, we derived projections of the relevant single-trial activity separately for each task and participant (Fig. 3*A*). From these projections, we then extracted the oscillatory power and phase during a pretarget period and determined for which time-frequency bins there was a significant relation between these and choice ("direct influence" model I; Fig. 3*B*). For both tasks, this revealed no effects of either power or phase on choice (Fig. 3*C*; at $P < 0.05$; here and in the following, all results are derived using cluster-based permutation controlling for multiple comparisons across time-frequency bins and are corrected for comparisons across regression models, parameters, and tasks using false discovery rate). We then asked whether pretarget activity was related to the sensory evidence (Y_{task}) encoded by the respective EEG components (model II; Fig. 3*C*). Indeed, for both tasks, this

relation was significant: for the frequency task at low frequencies (2–6 Hz, −0.6 to −0.1 s; $T_{sum} = 66$, $P = 0.001$) and the beta band (16–36 Hz, −0.3 to −0.1 s; $T_{sum} = 77$, $P = 0.002$), and for the intensity task in the alpha and beta bands (8–18 Hz, −0.6 to −0.1 s; $T_{sum} = 46$, $P = 0.01$). For neither task was there a significant effect of phase on evidence. Further, for both tasks, sensory evidence had a significant influence on choice [model III; frequency: $t(12) = 3.3$, $P = 0.006$; intensity: $t = 3.3$, $P = 0.006$], as expected from the neurobehavioral correlations reported above. Using additional analysis, we ruled out that systematic changes in the loudness of the acoustic background before the target sounds had a systematic influence on evidence or choice (cf. Fig. S1*B* and *SI Results*). These results suggest that pretarget activity in auditory networks has no direct effect on choice. Rather, the power in task-specific frequency bands influences the single-trial sensory evidence reflected by these networks, which in turn influences choice. Hence, any potential influence of power on choice (that may not have reached significance here) is likely mediated through an effect on sensory evidence.

Pretarget Influences in Frontoparietal Networks. For this EEG component, we found consistent effects of pretarget phase on choice (Fig. 4). For the frequency task this was prominent in the alpha band (7–14 Hz; −0.4 to −0.1 s; $T_{sum} = 5.0$, $P = 0.003$), and for the intensity task in the theta band (2–6 Hz; −0.6 to −0.1 s; $T_{sum} = 3.9$, $P = 0.005$). For the intensity task there was also an influence of alpha power on choice (10–16 Hz; −0.4 to −0.1 s; $T_{sum} = 31$, $P = 0.013$). Importantly, for neither task did we observe a significant effect of either phase or power on sensory evidence. In addition, for neither task did sensory evidence have a significant influence on choice, although the effect was close to significance for intensity [frequency: $t(12) = 1.1$, $P = 0.27$; intensity: $t = 2.1$, $P = 0.056$], similar as for the neurobehavioral correlations reported above. This suggests that the influence of pretarget phase on choice is unlikely to be mediated by an influence of phase on the sensory evidence carried by this frontoparietal component. However, to further rule out this option, we investigated the statistical mediation effect of phase and power on choice through evidence (cf. Fig. 3*B*). Mediation effects for the time-frequency clusters with significant choice influences were not significant for either power or phase in either of the two tasks (at $P < 0.05$). Again we ruled out an influence of background loudness on evidence or choice (cf. Fig. S1*B* and *SI Results*). These results suggest that pretarget influences emerging within frontoparietal networks are mediated by mechanisms not directly involving the sensory evidence but rather reflect later-activated and general decision-driving processes.

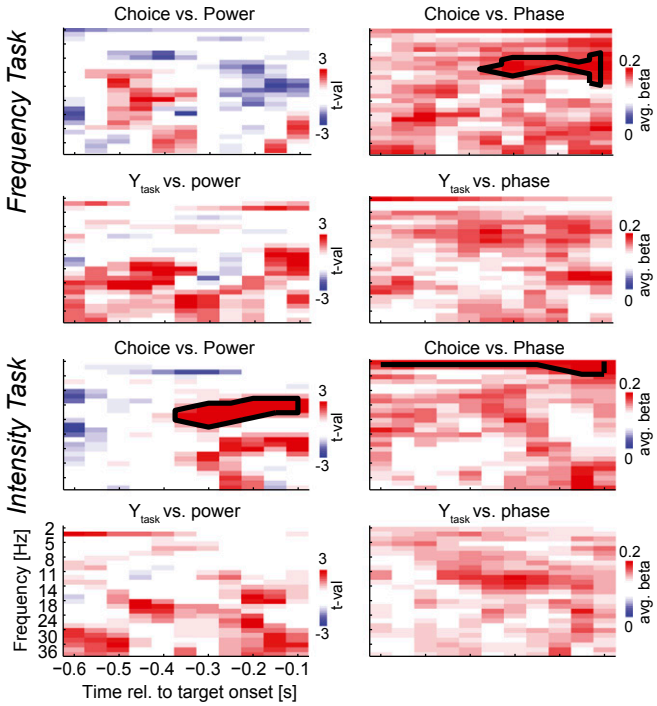

Fig. 4. Pretarget activity within frontoparietal networks and relation to choice. Group-level regression statistics for both tasks and models (as in Fig. 3) for the frontoparietal component. Significant time-frequency clusters are indicated in black ($P < 0.05$). The effect of sensory evidence on choice was not significant for either task (main text). Within these networks, phase had a direct effect on choice that was not mediated through sensory evidence.

Discussion

These results delineate two mechanisms by which prestimulus activity shapes perception consistently across tasks: one affecting the quality of early sensory representations by the power of rhythmic activity, and one involving changes in later decision-making processes aligned to the phase of delta and alpha activity. Thereby they reconcile previous reports in auditory studies by referring effects to two separate mechanisms. Further, they suggest that the observed variability in the relevant frequency bands arises from the engagement of distinct sensory and decision-related networks in each task.

Sensory and Decision-Related Origins of Prestimulus Influences. Rhythmic brain activity can affect the quality of early sensory representations (13, 25) and can influence decision criteria or the likelihood of evoking a motor response within frontoparietal areas (11, 26, 27). Using linear discriminant analysis, we were able to consistently separate earlier auditory from later-activated frontoparietal networks. This allowed us to separately quantify the impact of pretarget activity within these. Within auditory networks the sensory evidence was significantly related to perception, and hence pretarget activity could shape behavior via two distinct but not mutually exclusive mechanisms: via scaling the quality of sensory evidence or via another mechanism independent of the sensory input. We found that only power but not phase had an influence on the sensory decision process in these networks, and this was specific to the scaling of sensory evidence. Within later-activated frontoparietal networks, we found a consistent and direct influence of phase on choice. This was not mediated by sensory evidence, as shown by the weak influence of evidence on choice in this component and the absence of a statistical mediation effect. These results confirm previously described influences of oscillatory phase on hearing (4–7) and localize these to higher-level brain regions (see ref. 7 for a similar interpretation). In the intensity task, we also found a direct effect of alpha power on choice. Hence, depending on the task, both the amplitude and timing of oscillatory activity in frontoparietal networks can shape sensory decisions (see ref. 11 for a similar conclusion in the somatosensory system).

Studies on prestimulus influences in EEG activity have often focused on activity over selected electrodes, such as those carrying the strongest oscillatory power in a band of interest (28, 29) or those generally known to yield strong evoked responses for the modality of interest (6, 20). Our approach avoids these a priori assumptions by considering the activity in a linear EEG component, selected to recover the strongest EEG-based evidence for discriminating the task-relevant stimuli. As shown by recent work on the neural correlates of perceptual decisions (16–18, 27), such a signal-driven selection of neuroimaging activity may yield more powerful insights than the focus on individual electrodes, especially as it naturally accounts for intersubject variability and differences in task-relevant networks.

Previous studies using a target-in-background detection task found that performance varied systematically with the target

position relative to the background (4–6). We did not observe such an effect here. One explanation is that in contrast to the previous studies, target sounds were clearly audible and easy to localize in time, whereas the extraction of their relative features was difficult. A prominent theory suggests that the auditory system engages in a rhythmic listening mode aligned to sensory regularities when scanning complex scenes (30, 31). However, in the present paradigm, detection was easy and a rhythmic mode was possibly not engaged. As a result, we report the neural underpinnings of rhythmic perceptual gating when the auditory system is not entrained by the acoustic environment (9).

Reconciling Previous Work and Common Principles Across Modalities. Previous studies diverged as to the specific frequency bands in which prestimulus activity seems to guide perception. For example, auditory detection was shown to depend on theta power and phase (4), on delta phase (5, 6), or even on multifrequency states (9). Further, temporal predictions were reported to depend on delta and beta power and delta phase (19), whereas speech discrimination was found to vary with alpha phase (7). In the visual domain, alpha activity predicts detection performance via power (32, 33), phase (3), or both (34), and similar findings were reported in the somatosensory system (10, 11, 35). By directly comparing two tasks within the same participants, our results demonstrate consistent patterns of prestimulus influences (power–sensory evidence; phase–choice), but also show that the relevant frequency bands differ between tasks. Hence, the diversity of previous reports is most parsimoniously explained by differences in task-relevant networks that possibly engage neural activity at distinct timescales, and by the intermingling of sensory representations and choice-related activity in the analyzed signatures of brain activity.

In line with this, we found that the topographies of the relevant auditory components differed between tasks. This fits with the understanding that the processing of pitch and loudness may preferentially engage the ventral and dorsal auditory streams and their frontal projections (21, 36–38). In both tasks, sensory evidence was related to alpha/beta power. Previously, alpha power has been linked to listening effort in challenging environments (39) and may reflect the inhibition of interfering acoustic streams (40), whereas beta activity has been linked to corticocortical communication (10, 41). The observed alpha/beta effects could reflect intrinsic processes within early auditory regions, such as changes in the signal-to-noise ratio of sensory representations (13). However, we cannot rule out network-level effects such as changes in effective connectivity between auditory regions (10, 42). The phase of pretarget activity was relevant for perception only within the frontoparietal networks. Studies on perceptual decision making have described the rhythmic accumulation of sensory evidence (26) and implied rhythmic phase as critical for implementing the attentional selection in time (43). In line with this, our results provide strong evidence to support a high-level origin of prestimulus phase effects on perception. In the intensity task, we also observed an influence of alpha power on choice. Although we can only speculate as to the origin of this difference between tasks, changes in decision criteria with alpha power have been described previously (11, 27).

How does the absence of phase effects in the auditory component fit with studies showing that the phase of rhythmic auditory activity is dynamically aligned ("entrained") to acoustic regularities (44–46)? In principle, phase entrainment should lead to an influence of phase on subsequent stimuli, a mechanism that has been implied in the segmentation of acoustic scenes (47, 48). In the present study, perception and auditory activity were not strongly entrained by the background sound, and hence the mechanisms linking phase and neural gain were possibly not sufficiently engaged. The power of slow auditory cortical activity has been related to changes in background spiking activity (13). Background activity can change the quality of sensory representations similar to changes in sensory gain associated with phase (13), and this may be the explanation for the power dependency of sensory evidence reported here.

It is important to note that our results are based on detecting significant interactions between multiple variables. This leaves the possibility that weaker (here not significant) effects may exist. Furthermore, although the phase and power derived from the same signal are frequently interpreted as reflecting distinct neural processes, this may be ambiguous as to the underlying neural generators (cf. *SI Discussion*). Still, the present results show that the phase and power derived from the same band but within distinct task-relevant networks can reflect neural processes that contribute differentially to the sensory–decision cascade. Notably, the present results do not speak to the complementarity of the phase/power influences in the auditory and frontoparietal networks. Some studies have suggested that top–down interactions between cognitive processes and sensory regions determine the patterns of sensory encoding in sensory cortices (49, 50), and future work is required to investigate the possibility that the two mechanisms described here are part of the same large-scale process.

Materials and Methods

Data were obtained from 16 healthy adult participants following written informed consent. The study was conducted in accordance with the Declaration of Helsinki and was approved by the local ethics committee (College of Science and Engineering, University of Glasgow). See *SI Materials and Methods* for full details. In brief, we used two auditory discrimination tasks based on pure tone targets embedded in a background sound, similar to previous work (4) (Fig. 1*A*). In the frequency (intensity) task, subjects compared the pitch (loudness) of subsequent tones and judged which of the two was higher (louder). The second tone was always the standard, whereas the first was higher or lower, varying over seven different levels. These levels were equally spaced (in octaves or decibels) between a difference of 0 Hz (0 dB) and twice each participant's threshold. Frequency thresholds were 0.09 ± 0.103 octaves (mean ± SD) and intensity thresholds were 2.95 ± 1.60 dB. Data from three participants had to be excluded, and results are presented for the 13 participants who each performed both tasks reliably. We used multivariate discriminant analysis across all trials and stimulus levels to localize EEG components that discriminated the two stimulus conditions classified by the participants. Cluster analysis yielded three systematically different components (Fig. 2*C*), for each of which we derived neurometric curves and projections of single-trial activity. We exploited these projections as an estimator of the underlying task-relevant activity (17, 18, 51), and studied the relation between pretarget activity, sensory evidence (the projection value), and choice using multiple regression models (Fig. 3*B*): model I: logistic regression of choice on power/phase to determine whether state influences choice (as expected); and model II: linear regression of evidence on power/phase to test whether state influences sensory representations. Any potential effect of state on choice could possibly be mediated through an effect on evidence (direct and indirect pathways in Fig. 3*B*). Mediation analysis was used to dissociate these two possibilities (52) via a third model: model III: logistic regression of choice on evidence and power/phase. Group-level statistics was based on a cluster-based permutation procedure correcting for multiple comparisons across time-frequency bins (53) and further corrected for multiple comparisons across regression models, EEG components, and tasks using the false discovery rate (FDR; at $P < 0.05$).

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1. Jensen O, Bonnefond M, VanRullen R (2012) An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends Cogn Sci* 16(4):200–206.
2. Vanrullen R, Busch NA, Drewes J, Dubois J (2011) Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. *Front Psychol* 2:60.

3. Busch NA, Dubois J, VanRullen R (2009) The phase of ongoing EEG oscillations predicts visual perception. *J Neurosci* 29(24):7869–7876.
4. Ng BS, Schroeder T, Kayser C (2012) A precluding but not ensuring role of entrained low-frequency oscillations for auditory perception. *J Neurosci* 32(35):12268–12276.
5. Henry MJ, Herrmann B, Obleser J (2014) Entrained neural oscillations in multiple frequency bands comodulate behavior. *Proc Natl Acad Sci USA* 111(41):14935–14940.
6. Henry MJ, Obleser J (2012) Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. *Proc Natl Acad Sci USA* 109(49):20095–20100.
7. Strauß A, Henry MJ, Scharinger M, Obleser J (2015) Alpha phase determines successful lexical decision in noise. *J Neurosci* 35(7):3256–3262.
8. Neuling T, Rach S, Wagner S, Wolters CH, Herrmann CS (2012) Good vibrations: Oscillatory phase shapes perception. *Neuroimage* 63(2):771–778.
9. Henry MJ, Herrmann B, Obleser J (2016) Neural microstates govern perception of auditory input without rhythmic structure. *J Neurosci* 36(3):860–871.
10. Weisz N, et al. (2014) Prestimulus oscillatory power and connectivity patterns predispose conscious somatosensory perception. *Proc Natl Acad Sci USA* 111(4): E417–E425.
11. Baumgarten TJ, Schnitzler A, Lange J (2016) Prestimulus alpha power influences tactile temporal perceptual discrimination and confidence in decisions. *Cereb Cortex* 26(3):891–903.
12. Lakatos P, et al. (2005) An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *J Neurophysiol* 94(3):1904–1911.
13. Kayser C, Wilson C, Safaai H, Sakata S, Panzeri S (2015) Rhythmic auditory cortex activity at multiple timescales shapes stimulus-response gain and background firing. *J Neurosci* 35(20):7750–7762.
14. Reig R, Zerlaut Y, Vergara R, Destexhe A, Sanchez-Vives MV (2015) Gain modulation of synaptic inputs by network state in auditory cortex in vivo. *J Neurosci* 35(6): 2689–2702.
15. Haegens S, Nácher V, Luna R, Romo R, Jensen O (2011) α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc Natl Acad Sci USA* 108(48):19377–19382.
16. Mostert P, Kok P, de Lange FP (2015) Dissociating sensory from decision processes in human perceptual decision making. *Sci Rep* 5:18253.
17. Marti S, King JR, Dehaene S (2015) Time-resolved decoding of two processing chains during dual-task interference. *Neuron* 88(6):1297–1307.
18. Philiastides MG, Heekeren HR, Sajda P (2014) Human scalp potentials reflect a mixture of decision-related signals during perceptual choices. *J Neurosci* 34(50):16877–16889.
19. Arnal LH, Doelling KB, Poeppel D (2015) Delta-beta coupled oscillations underlie temporal prediction accuracy. *Cereb Cortex* 25(9):3077–3085.
20. Stefanics G, et al. (2010) Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. *J Neurosci* 30(41):13578–13585.
21. Belin P, et al. (1998) The functional anatomy of sound intensity discrimination. *J Neurosci* 18(16):6388–6394.
22. Zatorre RJ, Evans AC, Meyer E (1994) Neural mechanisms underlying melodic perception and memory for pitch. *J Neurosci* 14(4):1908–1919.
23. Giani AS, Belardinelli P, Ortiz E, Kleiner M, Noppeney U (2015) Detecting tones in complex auditory scenes. *Neuroimage* 122:203–213.
24. Gerson AD, Parra LC, Sajda P (2005) Cortical origins of response time variability during rapid discrimination of visual objects. *Neuroimage* 28(2):342–353.
25. McGinley MJ, David SV, McCormick DA (2015) Cortical membrane potential signature of optimal states for sensory signal detection. *Neuron* 87(1):179–192.
26. Wyart V, de Gardelle V, Scholl J, Summerfield C (2012) Rhythmic fluctuations in evidence accumulation during decision making in the human brain. *Neuron* 76(4): 847–858.
27. Lou B, Li Y, Philiastides MG, Sajda P (2014) Prestimulus alpha power predicts fidelity of sensory encoding in perceptual decision making. *Neuroimage* 87:242–251.
28. Busch NA, VanRullen R (2010) Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proc Natl Acad Sci USA* 107(37):16048–16053.
29. Thut G, Nietzel A, Brandt SA, Pascual-Leone A (2006) Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J Neurosci* 26(37):9494–9502.
30. Schroeder CE, Lakatos P (2009) Low-frequency neuronal oscillations as instruments of sensory selection. *Trends Neurosci* 32(1):9–18.
31. Lakatos P, et al. (2009) The leading sense: Supramodal control of neurophysiological context by attention. *Neuron* 64(3):419–430.
32. van Dijk H, Schoffelen JM, Oostenveld R, Jensen O (2008) Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *J Neurosci* 28(8): 1816–1823.
33. Romei V, et al. (2008) Spontaneous fluctuations in posterior alpha-band EEG activity reflect variability in excitability of human visual areas. *Cereb Cortex* 18(9):2010–2018.
34. Mathewson KE, Gratton G, Fabiani M, Beck DM, Ro T (2009) To see or not to see: Prestimulus alpha phase predicts visual awareness. *J Neurosci* 29(9):2725–2732.
35. Lange J, Halacz J, van Dijk H, Kahlbrock N, Schnitzler A (2012) Fluctuations of prestimulus oscillatory power predict subjective perception of tactile simultaneity. *Cereb Cortex* 22(11):2564–2574.
36. Hart HC, Palmer AR, Hall DA (2002) Heschl's gyrus is more sensitive to tone level than non-primary auditory cortex. *Hear Res* 171(1-2):177–190.
37. Hickok G, Poeppel D (2007) The cortical organization of speech processing. *Nat Rev Neurosci* 8(5):393–402.
38. Du Y, et al. (2015) Rapid tuning of auditory "what" and "where" pathways by training. *Cereb Cortex* 25(2):496–506.
39. Obleser J, Weisz N (2012) Suppressed alpha oscillations predict intelligibility of speech and its acoustic details. *Cereb Cortex* 22(11):2466–2477.
40. Strauß A, Wöstmann M, Obleser J (2014) Cortical alpha oscillations as a tool for auditory selective inhibition. *Front Hum Neurosci* 8:350.
41. Arnal LH, Wyart V, Giraud AL (2011) Transitions in neural oscillations reflect prediction errors generated in audiovisual speech. *Nat Neurosci* 14(6):797–801.
42. Bowers AL, Saltuklaroglu T, Harkrider A, Wilson M, Toner MA (2014) Dynamic modulation of shared sensory and motor cortical rhythms mediates speech and nonspeech discrimination performance. *Front Psychol* 5:366.
43. Landau AN, Schreyer HM, van Pelt S, Fries P (2015) Distributed attention is implemented through theta-rhythmic gamma modulation. *Curr Biol* 25(17):2332–2337.
44. Ng BSW, Logothetis NK, Kayser C (2013) EEG phase patterns reflect the selectivity of neural firing. *Cereb Cortex* 23(2):389–398.
45. Kayser C, Montemurro MA, Logothetis NK, Panzeri S (2009) Spike-phase coding boosts and stabilizes information carried by spatial and temporal spike patterns. *Neuron* 61(4):597–608.
46. Schroeder CE, Lakatos P, Kajikawa Y, Partan S, Puce A (2008) Neuronal oscillations and visual amplification of speech. *Trends Cogn Sci* 12(3):106–113.
47. Peelle JE, Davis MH (2012) Neural oscillations carry speech rhythm through to comprehension. *Front Psychol* 3:320.
48. Giraud AL, Poeppel D (2012) Cortical oscillations and speech processing: Emerging computational principles and operations. *Nat Neurosci* 15(4):511–517.
49. Nienborg H, Cumming BG (2009) Decision-related activity in sensory neurons reflects more than a neuron's causal effect. *Nature* 459(7243):89–92.
50. Nienborg H, Roelfsema PR (2015) Belief states as a framework to explain extra-retinal influences in visual cortex. *Curr Opin Neurobiol* 32:45–52.
51. Parra LC, Spence CD, Gerson AD, Sajda P (2005) Recipes for the linear analysis of EEG. *Neuroimage* 28(2):326–341.
52. MacKinnon DP, Fairchild AJ, Fritz MS (2007) Mediation analysis. *Annu Rev Psychol* 58: 593–614.
53. Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Methods* 164(1):177–190.
54. Oostenveld R, Fries P, Maris E, Schoffelen JM (2011) FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell Neurosci* 2011:156869.
55. Debener S, Thorne JD, Schneider TR, Viola FC (2010) Using ICA for the analysis of multi-channel EEG data. Simultaneous EEG and fMRI: Recording, Analysis, and Application, eds Ullsperger M, Debener S (Oxford Univ Press, Oxford), pp 121–134.
56. Hipp JF, Siegel M (2013) Dissociating neuronal gamma-band activity from cranial and ocular muscle activity in EEG. *Front Hum Neurosci* 7:338.
57. O'Beirne GA, Patuzzi RB (1999) Basic properties of the sound-evoked post-auricular muscle response (PAMR). *Hear Res* 138(1-2):115–132.
58. Keren AS, Yuval-Greenberg S, Deouell LY (2010) Saccadic spike potentials in gamma-band EEG: Characterization, detection and suppression. *Neuroimage* 49(3): 2248–2263.
59. Blankertz B, Lemm S, Treder M, Haufe S, Müller KR (2011) Single-trial analysis and classification of ERP components—A tutorial. *Neuroimage* 56(2):814–825.
60. Nichols TE, Holmes AP (2002) Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Hum Brain Mapp* 15(1):1–25.
61. Henry MJ, Herrmann B (2014) Low-frequency neural oscillations support dynamic attending in temporal context. *Timing Time Percept* 2(1):62–86.
62. Whittingstall K, Logothetis NK (2009) Frequency-band coupling in surface EEG reflects spiking activity in monkey visual cortex. *Neuron* 64(2):281–289.
63. Einevoll GT, Kayser C, Logothetis NK, Panzeri S (2013) Modelling and analysis of local field potentials for studying the function of cortical circuits. *Nat Rev Neurosci* 14(11): 770–785.
64. Panzeri S, Macke JH, Gross J, Kayser C (2015) Neural population coding: Combining insights from microscopic and mass signals. *Trends Cogn Sci* 19(3):162–172.
65. Mazzoni A, et al. (2015) Computing the local field potential (LFP) from integrate-and-fire network models. *PLOS Comput Biol* 11(12):e1004584.