Tuning alpha rhythms to shape conscious visual perception

Highlights

- Neural mechanisms of visual processing and its interpretation are dissociable
- Different alpha parameters can be selectively modulated by rhythmic-TMS
- Individual alpha frequency causally shapes objective accuracy
- Alpha amplitude predicts subjective confidence and metacognitive abilities

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In brief

Di Gregorio, Trajkovic et al. empirically identify the neural substrates of objective accuracy and subjective representation and interpretation of sensory events, demonstrating that they can be causally dissociated. They show alpha frequency to engender discrete sensory sampling and alpha amplitude to shape perceptual decision-making processes.
Tuning alpha rhythms to shape conscious visual perception

Francesco Di Gregorio, Jelena Trajkovic, Cristina Roperti, Eleonora Marcantoni, Paolo Di Luzio, Alessio Avenanti, Gregor Thut, and Vincenzo Romei

SUMMARY

It is commonly held that what we see and what we believe we see are overlapping phenomena. However, dissociations between sensory events and their subjective interpretation occur in the general population and in clinical disorders, raising the question as to whether perceptual accuracy and its subjective interpretation represent mechanistically dissociable events. Here, we uncover the role that alpha oscillations play in shaping these two indices of human conscious experience. We used electroencephalography (EEG) to measure occipital alpha oscillations during a visual detection task, which were then entrained using rhythmic-TMS. We found that controlling prestimulus alpha frequency by rhythmic-TMS modulated perceptual accuracy, but not subjective confidence in it, whereas controlling poststimulus (but not prestimulus) alpha amplitude modulated how well subjective confidence judgments can distinguish between correct and incorrect decision, but not accuracy. These findings provide the first causal evidence of a double dissociation between alpha speed and alpha amplitude, linking alpha frequency to spatiotemporal sampling resources and alpha amplitude to the internal, subjective representation and interpretation of sensory events.

INTRODUCTION

The well-known axiom “seeing is believing” implies that what we see and what we believe we see are largely overlapping phenomena. However, there are many examples of dissociations between sensory events and their subjective interpretation, both in the general population (i.e., false memories) and in the subclinical and clinical psychiatric populations (e.g., schizophrenia). A key question, therefore, is whether perceptual accuracy and its subjective interpretation represent mechanistically dissociable events of our conscious experience, and, if so, what their neural underpinnings might be.

Alpha oscillations (range 7–13 Hz) in the human brain may play an active role in both sensory processing and conscious perception. In particular, prestimulus alpha amplitude has been shown to account for a momentary level of cortical excitability and to predict subjective confidence in response to visual stimuli. Specifically, higher levels of alpha amplitude seem to account for reduced subjective confidence and reduced proneness to reporting a visual percepts (more conservative decision criterion), without affecting the level of accuracy of the response. These new insights into the role of alpha amplitude in perception suggest that alpha amplitude might not primarily reflect perceptual accuracy but rather a change in the internal response criterion. However, this leaves open a fundamental question: what are the oscillatory correlates of perceptual accuracy?

Recent reports have highlighted the relevance of alpha frequency in perceptual sampling, with faster alpha oscillations resulting in higher temporal resolution and more accurate perceptual experience, potentially through an increased accumulation of sensory evidence over time. Importantly, we hypothesize here that this higher temporal resolution of visual sampling can successfully translate into higher accuracy in general, by allocating more resources to the perceptually relevant sensory dimension within the same amount of time.

Here, in a first experiment, we have used a visual detection task with spatially lateralized stimuli and electroencephalography (EEG) to directly test the hypotheses that (1) alpha frequency accounts for objective accuracy (correct versus
erroneous responses and d’ measures\(^{28}\), while (2) alpha amplitude predicts subjective confidence (low versus high confidence responses) and/or (3) relates to metacognitive abilities, i.e., how well subjective confidence judgments can distinguish between correct and incorrect decisions (as indexed by meta-d’ measures\(^{28}\)).

Crucially, in a second experiment, we used rhythmic transcranial magnetic stimulation (rhythmic-TMS) prior to stimulus onset around individual alpha frequency (IAF) to entrain prestimulus oscillatory activity in the alpha band toward slower or faster alpha frequency or higher alpha amplitudes to influence individual performance toward lower or higher accuracy or to impact individual subjective confidence levels, respectively.

Finally, because stimulus processing has been shown to influence metacognitive abilities,\(^{30-32}\) in a third experiment, we delivered rhythmic-TMS at each participant’s own IAF poststimulus but prior to a subjective confidence prompt to test how increases in poststimulus alpha amplitude can modulate their ability to distinguish between correct and incorrect decisions, measured by means of meta d’.

RESULTS

A total of 92 participants took part in three experiments (Figure 1), designed to map prestimulus alpha frequency and alpha amplitude on objective versus subjective performance measures (EEG experiment 1) and to test for their causative relationships (TMS-EEG experiments 2 and 3).

Alpha frequency and alpha amplitude dissociate with respect to objective accuracy, subjective confidence, and metacognitive abilities

In experiment 1, 24 participants (12 women; mean age = 23.2, SE = 2.61) performed a visual detection task (Figure 1A) in which lateralized stimuli (8 x 8 checkboard squares) were preceded by a spatially uninformative cue (an X), indicating that a stimulus will be occurring in the lower left or right hemifield with 50% probability (chance level). Each black and white checkboard was flashed for 60 ms and could contain isoluminant gray circles, the contrast of which was set for each individual to their 50% perceptual threshold. Half of the trials were catch trials, i.e., checkboard squares without any gray circle embedded in them (see STAR Methods for details).

Participants were instructed to respond whenever they perceived gray circles within the lateralized checkboarders. Following this primary task and about 1.5-2 s poststimulus, they were prompted to indicate on a scale of 1 to 4 how confident they were of their percept, with (1) representing “no confidence at all,” (2) “little confidence,” (3) “moderate confidence,” and (4) “high confidence” (see Figure 1A). EEG signals were concurrently recorded from 64 electrodes while this task was performed (see STAR Methods).

Prestimulus alpha frequency and accuracy

We looked at whether correct versus erroneous responses could be best explained by the frequency of alpha oscillations prior to stimulus presentation, rather than by their amplitude. Our analysis of prestimulus alpha frequency (Figure 2A) showed a significant main effect of ACCURACY (Correct versus Errors) \((F(1,23) = 18.2, p < 0.001,\) and partial eta squared \((\eta_{p}^{2} = 0.442)\). This result suggests that individual prestimulus alpha frequency can differentiate between correct and erroneous responses, with faster alpha frequency predicting correct responses \((M = 11.45 Hz, SE = 0.18 Hz)\) and slower alpha frequency predicting errors \((M = 11.02 Hz, SE = 0.18 Hz)\). Moreover, the effect of alpha frequency was maximal over the posterior electrodes (Figure 2A, map inset), involving left and right sites equally as no main effect of HEMISPHERE (ipsilateral versus contralateral to the presented stimulus) \((F(1,23) = 1.34, p = 0.259,\) and \(\eta_{p}^{2} = 0.06)\) nor a significant interaction of ACCURACY x HEMISPHERE \((F(1,23) = 0.33, p = 0.571,\) and \(\eta_{p}^{2} = 0.014)\) was found.

We further tested whether prestimulus alpha frequency can predict individual performance across participants as assessed by d’, a sensitivity index that takes into account both correct responses and false alarms, and thus, — relative to the simple hit rate measure — has the advantage of discounting any potential effect of response bias, with higher values reflecting higher task accuracy.\(^{28}\) Using a median-split procedure for d’ scores, we divided participants in two numerically equivalent groups (high versus low d’). In line with our hypothesis, a between-groups analysis of alpha frequency shows faster prestimulus alpha frequency in the high d’ group \((11.55 Hz, SE = 0.22 Hz)\) compared with the low d’ group \((10.29 Hz, SE = 0.66 Hz)\) by 1.26 Hz: \(\eta_{p}^{2}(22) = 1.832, p = 0.040,\) and Cohen d \((d) = 0.374)\) (one-tailed unpaired two-sample t test).

In contrast, the analysis of both pre- and poststimulus alpha amplitude (see Figure S1B) showed no significant effects on ACCURACY \((all F_s(1,23) < 3.05, all p_s > 0.094, all \eta_{p}^{2} < 0.117)\), in line with recent reports that alpha amplitude does not account for objective accuracy.\(^{6,17,18,30}\)

Prestimulus alpha amplitude and confidence

We then tested whether prestimulus alpha amplitude, rather than alpha frequency, could account for confidence judgments\(^{6,17,18}\) (Figure 2B). We found a main effect of CONFIDENCE \((F(1,23) = 9.03, p = 0.006,\) and \(\eta_{p}^{2} = 0.282)\), with desynchronized alpha amplitude in high confidence trials \((-0.699 dB, SE = 0.409 dB)\) and synchronized alpha amplitude in low confidence trials \((0.719 dB, SE = 0.251 dB)\), suggesting that alpha amplitude has a significant impact on perceptual confidence. Moreover, topography (Figure 2B, map inset) shows posterior alpha amplitude modulations with an even distribution across hemispheres, indicating no main effect of HEMISPHERE (ipsilateral versus contralateral to the presented stimulus) \((F(1,23) = 0.201, p = 0.658,\) and \(\eta_{p}^{2} = 0.009)\) nor a significant interaction of CONFIDENCE x HEMISPHERE \((F(1,23) = 1.323, p = 0.262,\) and \(\eta_{p}^{2} = 0.054)\).

For completeness, control analyses performed on prestimulus alpha frequency (see Figure S1A) showed no main effect of CONFIDENCE nor any interaction with HEMISPHERE \((all F_s(1,23) < 0.47, p_s > 0.658,\) and \(\eta_{p}^{2} < 0.699 dB, SE = 0.409 dB)\).

Poststimulus alpha amplitude, confidence, and meta d’

Following stimulus presentation, as the initial choice on decisions and confidence continue to evolve,\(^{31,32}\) we asked whether subjective confidence judgments are influenced by postperceptual processes. To this aim, we analyzed alpha amplitude in a time window after stimulus presentation \((0-900 ms)\), corresponding
to a poststimulus time period but before the confidence prompt (Figure 2C). The analysis of poststimulus alpha amplitude revealed a main effect of CONFIDENCE ($F(1,23) = 4.367, \ p = 0.048$, and $\eta_p^2 = 0.16$), with more desynchronized alpha amplitude in high confidence trials (−3.41 dB, SE = 0.38 dB) compared with low confidence trials (−3.08 dB, SE = 0.34 dB). Moreover, the analyses showed a main effect of HEMISPHERE ($F(1,23) = 5.358, \ p = 0.03$, and $\eta_p^2 = 0.189$) and most importantly,
an interaction of CONFIDENCE × HEMISPHERE ($F(1,23) = 4.347$, $p = 0.048$, and $\eta^2_p = 0.159$), showing that when looking at post stimulus alpha amplitude, the confidence effects are accounted for by the contralateral (high confidence = −3.64 dB, SE = 0.396 dB; low confidence = −3.14 dB, SE = 0.347 dB; $t(23) = 2.747, p = 0.011$, and $d = 0.586$) but not the ipsilateral hemisphere (high confidence = −3.17 dB, SE = 0.387 dB; low confidence = −3.01 dB, SE = 0.349 dB; $t(23) = 0.906$, $p = 0.375$, and $d = 0.193$). These findings suggest that poststimulus alpha amplitude has a retinotopic distribution being modulated by the stimulus position. Indeed, while the relationship between confidence levels and prestimulus alpha amplitude can be observed for both hemispheres, only contralateral alpha amplitude accounts for individual confidence levels after stimulus presentation.

We then tested whether poststimulus alpha amplitude could specifically account for metacognitive abilities. In other words, we tested how well subjective confidence judgments can distinguish between correct and incorrect decisions by means of meta $d'$, a measure that quantifies metacognitive performance and that reflects the efficacy of confidence ratings to discriminate objectively correct from erroneous responses. In a between-subject design, by using a median-split procedure, we divided participants with high and low metacognitive abilities. We found that poststimulus alpha amplitude in the high meta-$d'$ group was significantly more desynchronized (−4.66 dB, $SE = 0.59$ dB) relative to the low meta-$d'$ group (−3.26 dB, $SE = 0.39$ dB; one-tailed unpaired two-sample $t$ test: $t(22) = 1.966$, $p = 0.031$, and $d = 0.567$), thus supporting the idea that poststimulus alpha amplitude can predict metacognitive performance. Moreover, this role seems specific for poststimulus alpha amplitude because prestimulus changes of alpha amplitude could not account for between-subject differences in metacognition ($t(22) = 0.929$, $p = 0.181$, and $d = 0.189$), further supporting this interpretation.

Overall, these EEG results implicate alpha frequency in the level of objective accuracy, with higher alpha frequency accounting for higher accuracy but playing no role in determining one’s individual perceptual confidence. Conversely, alpha amplitude is implicated in perceptual decision confidence but has no role to play in objective accuracy. In sum, these results point to a functional dissociation of the two oscillatory markers, alpha frequency and alpha amplitude, which appear to shape sensory sampling and the subjective readout of this sampling, respectively.

**Entraining faster versus slower prestimulus alpha oscillations selectively shapes objective accuracy**

In experiment 2, we tested for the causal involvement of alpha frequency and alpha amplitude in objective accuracy versus...
confidence by using rhythmic-TMS to entrain alpha oscillations while participants performed the same visual task as in experiment 1 (Figure 1B). In three different experimental groups (n = 3 × 17 participants; 25 women; mean age = 23.39, SE = 0.36), we recorded EEG activity while concurrently administering 5-pulse rhythmic-TMS trains of fixed intensity (60% of the maximum stimulator output) to the right occipital cortex (coil placement over O2) prior to stimulus presentation. In the IAF ± 1 Hz groups, rhythmic-TMS frequency was set at 1 Hz faster/slower than the individual participant’s alpha frequency, which should entrain their alpha oscillations toward a faster/slower pace, respectively. In the IAF group, the rhythmic-TMS frequency was aligned with the participant’s alpha frequency. This has been shown to lead to enhanced alpha amplitude by entrainment and, thus, should have an impact on confidence rather than on accuracy. Together with active rhythmic-TMS, we employed sham stimulation at a matching frequency for every participant in each group to account for any nonspecific effects of rhythmic-TMS.

Perceptual accuracy was quantified via d’ score shown to be a more sensitive measure relative to hit rates, whereas task confidence was estimated via mean confidence and meta d’. All measures were analyzed across the two hemifields (left versus right), the two stimulation types (active rhythmic-TMS versus sham), and the three groups of participants (stimulated at IAF ± 1 Hz and IAF).

We looked at the impact of rhythmic-TMS on EEG activity across the three groups (Figure 3). As expected, prestimulus alpha frequency was modulated differently in active rhythmic-TMS versus sham stimulation across the experimental groups, depending on the recording site (STIMULATION × GROUP × HEMISPHERE interaction: F(2, 48) = 4.05, p = 0.024, and h² = 0.144). Specifically, stimulating at the lower alpha frequency slowed down prestimulus alpha activity during active rhythmic-TMS (M = 9.74 Hz, SE = 0.20), relative to sham stimulation (M = 10.66 Hz, SE = 0.20), selectively at the right (stimulated) alpha band 7–13 Hz in the prestimulus period (-500–0) (Figure 3A). (Lower) Violin plots report peak frequency during TMS and SHAM for each group (IAF = 1 Hz, IAF) and for the left and right (stimulated) hemispheres. Data are presented as median (full line) ± 1 quartile (dashed line). The topography image represents the difference in alpha frequency between TMS and SHAM stimulations.

Figure 3. Results of experiment 2: Rhythmic-TMS entrainment modulates EEG alpha frequency and its amplitude

Results are shown for each group performing the task in experiment 2 under different rhythmic-TMS alpha entrainment protocols (IAF = 1 Hz, IAF) (A) (Upper) Averaged alpha frequency is represented as the Z-scored mean power (10*log10[µV²/Hz]) spectrum during rhythmic-TMS in the prestimulus time period (-650–0) in the right (stimulated) hemisphere (electrode cluster: O2, PO4, and PO8) and left (nonstimulated) hemisphere (electrode cluster: O1, PO3, and PO7), for active rhythmic-TMS (TMS) and SHAM-control stimulations. (Lower) Violin plots report peak frequency during TMS and SHAM for each group (IAF = 1 Hz, IAF) and for the left and right (stimulated) hemispheres. Data are presented as median (full line) ± 1 quartile (dashed line). The topography image represents the difference in alpha frequency between TMS and SHAM stimulations. (B) (Upper) Prestimulus alpha amplitude is presented as time-frequency plots for each group (IAF = 1 Hz, IAF) of the difference between TMS and SHAM stimulations in the right (stimulated) hemisphere (electrode cluster: O2, PO4, and PO8) and in the left (nonstimulated) hemisphere (electrode cluster: O1, PO3, and PO7). Black boxes denote regions of statistical analyses (alpha band 7–13 Hz in the prestimulus period [-500–0]). (Lower) Violin plots report alpha power during TMS and SHAM for each group and for the left and right (stimulated) hemispheres. Data are presented as median (full line) ± 1 quartile (dashed line). Topography represents the difference in alpha frequency between TMS and SHAM stimulations. Two-tailed t test statistical significance is reported (*p < 0.05). Error bars represent standard error of the mean. A.U., arbitrary units; Diff, difference; µV, microvolt; Hz, hertz; ms, milliseconds; dB, decibel.

See also Figure S2.
at the site of stimulation (HEMISPHERE × STIMULATION interaction: \(F(1,48) = 6.36, p = 0.015\), and \(\eta^2_p = 0.117\)) and at the entrained rhythm (see Figure S3A).

In contrast, the broadband alpha amplitude (see Figure S3B) did not differ significantly across the three groups during the entrainment protocol (HEMISPHERE × STIMULATION × GROUP interaction: \(F(2,48) = 0.19, p = 0.830\), and \(\eta^2_p = 0.008\)). However, the entrainment effect on alpha amplitude (quantified via the difference between active rhythmic-TMS and sham stimulation) was largest at the frequency of stimulation (FREQUENCY × GROUP interaction: \(F(4,96) = 5.640, p < 0.001\), and \(\eta^2_p = 0.19\), for details, see Figure S2).

When examining the impact of entrainment on behavior (Figure 4A), we found that speeding up or slowing down alpha oscillations had a direct impact on performance (STIMULATION × GROUP × HEMIFIELD interaction \(F(1,48) = 3.25, p = 0.047\), and \(\eta^2_p = 0.119\)). Specifically, slowing down prestimulus alpha frequency led to lower \(d'\) scores in the active rhythmic-TMS and sham stimulation condition (relative to sham stimulation), exclusively in the hemifield contralateral to stimulation (\(t(16) = 2.67, p = 0.017\), and \(d = 0.65\)). In contrast, speeding up prestimulus alpha frequency led to higher \(d'\) values during active rhythmic-TMS (relative to sham stimulation), exclusively in the contralateral hemifield (\(t(16) = 2.52, p = 0.023\), and \(d = 0.61\)). Finally, entrainment at individual alpha frequencies did not yield differences in task accuracy, as predicted (all \(ts(16) < 1.19\), all \(ps > 0.252\), and all \(ds < 0.29\)). We further tested whether the impact of rhythmic-TMS on EEG oscillatory activity could account for the magnitude of the behavioral modulation induced by the TMS protocol (Figure 4B). To do so, we examined the relationship between sham-corrected performance and sham-corrected entrained frequency across participants (IAF ± 1 Hz groups included). The results reveal that a significant positive relationship exists between the TMS-induced change in oscillatory peak frequency and performance gain (\(R^2 = 0.29, p = 0.001\)), further confirming a link between alpha frequency and performance accuracy.

Our results thus far indicate that prestimulus alpha frequency, but not alpha amplitude, has a causative role in sampling sensory input, accounting for visual accuracy.

Alpha amplitude dynamics shape subjective confidence and metacognition, not accuracy

Another goal of experiment 2 was to determine whether alpha amplitude dynamics causally shape subjective representation and interpretation of perceptual performance. However, confidence levels and metacognitive abilities—as measured via confidence mean and meta-\(d'\) scores, respectively—appeared not to be affected across the three different stimulation protocols nor between the two hemifields because neither the main effects of GROUP, HEMIFIELD, and STIMULATION nor their interactions reached significance (all \(Fs(2,48) < 2.72, all ps > 0.076\), and all \(\eta^2_p < 0.102\)). The short-term nature of entrainment effects might explain these null results because they are limited to a few hundreds of milliseconds following stimulation. 37,39,40 This is long enough for prestimulus TMS entrainment to influence the primary accuracy response because this was collected immediately after stimulus presentation. The secondary, higher decision confidence response, however, which was associated with prestimulus EEG alpha amplitude, was collected only at 1.5–2 s post-stimulus (through the confidence prompt) and hence, occurred >1 s after rhythmic-TMS offset (see Figure 1B), when entrainment effects might not be sufficiently sustained anymore. 37,41 Therefore, to further assess the causal role of alpha amplitude dynamics in perceptual awareness, and particularly in metacognitive abilities, we ran a third follow-up experiment aimed at entraining poststimulus alpha amplitude in 17 participants (12 women; mean age = 22.47, SE = 0.66). This group received 5-pulse rhythmic-TMS trains that were tailored to their IAF with pulses applied just before the confidence prompt, i.e. after stimulus presentation. We further tested whether the impact of rhythmic-TMS on EEG oscillatory activity could account for the magnitude of the behavioral modulation induced by the TMS protocol (Figure 4B). To do so, we examined the relationship between sham-corrected performance and sham-corrected entrained frequency across participants (IAF ± 1 Hz groups included). The results reveal that a significant positive relationship exists between the TMS-induced change in oscillatory peak frequency and performance gain (\(R^2 = 0.29, p = 0.001\)), further confirming a link between alpha frequency and performance accuracy.

EEG analyses in experiment 3 revealed a maximal entrainment effect in broadband alpha amplitude prior to the confidence...
prompt during active rhythmic-TMS relative to sham stimulation at the stimulated site (HEMISPHERE × STIMULATION interaction: $F(1,16) = 6.91, p = 0.022$, and $\eta^2 = 0.302$). Moreover, as expected, the rhythmic-TMS trains at IAF did not have any effect on the alpha frequency measured prior to confidence judgment (all $Fs(1,16) < 0.19$, all $ps > 0.666$, and all $\eta^2 < 0.012$) (Figures 5A and 5B). Crucially, this selective modulation of alpha amplitude right before confidence judgment allowed us to causally test the impact of alpha amplitude on metacognitive abilities versus subjective confidence ratings. Our results show clear effects on metacognition, as highlighted by distinct modulations of meta-d’ scores, between active rhythmic-TMS and sham stimulation, depending on hemisphere (HEMIFIELD × STIMULATION interaction: $F(1,16) = 4.73, p = 0.045$, and $\eta^2 = 0.228$) (Figure 5C). Specifically, higher alpha amplitudes prior to the confidence prompt led to lower meta-d’ scores during active rhythmic-TMS versus sham stimulation, exclusively in the contralateral hemisphere ($t(16) = 2.74, p = 0.014$, and $d = 0.66$). Importantly, these induced changes in poststimulus alpha amplitude had a selective impact on metacognitive abilities and not on confidence measures or on perceptual accuracy (all $Fs(1,16) < 0.82$, all $ps > 0.379$, and all $\eta^2 < 0.049$), thus confirming the role of poststimulus alpha amplitude in higher-level postperceptual decision making.

Finally, we tested whether individual differences in TMS-induced poststimulus alpha amplitude modulations could account for the level of metacognitive abilities. To do so, we analyzed the relationship between sham-controlled TMS-induced alpha amplitude and sham-controlled meta-d’ levels for stimuli presented in the contralateral hemisphere. We found a significant inverse relationship, confirming that the higher the impact of rhythmic-TMS on alpha amplitude, the lower the resulting level of metacognition of the individual response ($R^2 = 0.27, p = 0.032$; Figure 5D). These results strongly support a role of poststimulus alpha amplitude in selectively shaping our metacognitive abilities, with higher poststimulus alpha amplitude leading to lower metacognition.
DISCUSSION

The oscillatory underpinnings of conscious perception have been the focus of many studies, yet they remain largely unknown. A number of studies have previously reported that prestimulus alpha oscillations over occipital sites might play a role in human perceptual performance prediction, highlighting the potential existence of a direct link between levels of alpha activity, cortical excitability, and perceptual sensitivity. Recent findings have, however, challenged these past interpretations and have highlighted the need to dissociate the processes that shape perceptual sensitivity from those that shape the subjective interpretation of a sensory event. Here, we disentangle the oscillatory dynamics of these two processes and go beyond a correlative approach. By using an information-based rhythmic-TMS protocol, we demonstrate that distinct markers of alpha activity have a causal role in shaping our conscious perception, a role that goes beyond that of a simple epiphenomenon. By directly manipulating alpha frequency and amplitude at the site of stimulation, we were able to dissociate perceptual sensitivity from the subjective representation and interpretation of a sensory event and thus, demonstrating their dualistic nature.

Our findings show that the speed of occipital alpha activity has a crucial and selective role in modulating perceptual sensitivity. This adds to previous reports showing that alpha cycles account for sampling sensory information into discrete units/perceptual frames (initially proposed by Varela et al. and reviewed by VanRullen [15]). From this, one might expect that higher frequency would translate in higher accuracy when information can be sampled over many cycles. However, why would this effect show even when a sensitively short-lasting stimulus, certainly shorter than one alpha cycle, is presented, as in our case? With our experimental design (60 ms stimulus duration), there is only one chance (sample) to capture the stimulus within an alpha cycle, and what would this tell us about the underlying mechanism? To address this, we provide here an exemplar account of the impact of frequency variations on sampling efficacy for a 9 and 11 Hz alpha oscillation. For these oscillations, cycles will range between 110 ms (for 9 Hz IAF) and 90 ms (for 11 Hz IAF). However, processing abilities will vary within the cycle, with a rapid fluctuation from a high-to-low excitability phase (alpha peak to trough). Thus, sampling is expected to occur in one-half of this cycle only, i.e., during ~ 55 ms for 9 Hz and ~ 45 ms for 11 Hz, respectively. Our data suggest that this sampling is more effective with lower alpha frequencies, even with stimuli as short as 60 ms, suggesting that evidence accumulation already starts to differ within one sampling sweep across variations of alpha frequencies. This can be explained by enhanced processing capacities for shorter than longer cycles because with the shorter sampling phases (~ 45 ms), our short-lasting stimulus (60 ms) is likely to be fully comprehended in one perceptual frame. For stimuli of longer durations (e.g., 1,000 ms), one would expect repeated sampling sweeps to further add to this difference because more full-sample sweeps can be packed in 1 s at higher than lower frequencies (11 versus 9 sweeps, for 11 versus 9 Hz). In sum, in this study, we claim that in line with existing literature, higher frequencies are expected to aid temporal resolution by creating more sampling frames per second; however, our data show that, at the same time, in the context of our specific experiment, higher frequency also means that less time is employed to create a single sampling frame, leading to higher processing capacities.

Furthermore, our EEG findings show an inverse relationship between levels of alpha amplitude and subjective confidence confirming previous findings. Indeed, prestimulus alpha amplitude has been proposed to relate to internal decision-making variables, rather than perceptual accuracy per se. However, our experimental manipulation by rhythmic-TMS could not verify the existence of a causal link between prestimulus alpha amplitude and confidence. However, several studies have concluded that our sense of confidence is also determined by processes that occur after we make a choice, thus integrating sensory evidence and improving our “metacognitive accuracy,” namely, the extent to which our confidence is consistent with our probability of being correct. Examining poststimulus alpha amplitude, experiments 1 and 3 demonstrate that after lateralized stimuli are presented, perceptually relevant, poststimulus alpha amplitude becomes focused in the hemisphere contralateral to stimulus presentation, with lower alpha amplitude leading to higher perceptual confidence. Moreover, these levels of poststimulus alpha desynchronization directly account for metacognitive abilities across participants and can be causally manipulated by rhythmic-TMS. These latter results suggest that poststimulus alpha modulations may reflect the integration of confidence judgment with the accumulated evidence after stimulus presentation to update and adjust metacognitive decisions. Taken together, these results speak in favor of a relevant role of alpha amplitude in postperceptual decision making. Therefore, it might be possible that prestimulus alpha amplitude dictates the initial level of perceptual bias (effects observed for confidence bilaterally, but not metacognitive effects) that subsequently integrates sensory evidence brought by the stimulus itself (reflected in hemisphere-specific processes), resulting in postperceptual estimation of the performance.

While our experiments show that alpha frequency and amplitude, and hence sensitivity and confidence, are dissociable entities, these processes likely work in concert in more ecological situations to maximize the efficiency of our conscious experience. We observed that the entrainment effects on oscillation and perception showed corresponding topographic/retinotopic distributions, with perception being exclusively modulated in the hemifield contralateral to the stimulated site, suggesting that the oscillatory substrates of effective sampling and subjective confidence could be oriented in space to optimize the allocation of attention resources. Therefore, under controlled conditions (for example, by presenting informative cues or in predictive contexts that are associated with spatial priors), one might expect the spatially specific co-occurrence of alpha frequency and amplitude modulation that is contralateral to the to-be-attended or expected location. Future research into the interdependency of these two circuits may shed new light on different neuropsychological phenomena. For example, the failure to integrate perceptual processes and their subjective interpretation might lead to altered cognitive experiences, such as confabulations or the formation of false representations and memories, with relevant implications.
for clinical and forensic neuropsychology. The failure to integrate perceptual processes and their subjective interpretation may also lead to conscious departure from sensory events in patients with acute schizophrenia.61

In conclusion, our results point to a functional dissociation between the accuracy of what we see and our interpretation of it. We reveal that the sampling of visual information and its subjective interpretation, which are strongly interdependent in everyday life, are dissociable in terms of neural mechanisms in oscillatory activity. Specifically, alpha frequency and amplitude reflect the activity of these two independent mechanisms that serve complementary functions. Alpha frequency represents a spatial and temporal sampling mechanism27,62–64 that shapes perceptual sensitivity. In contrast, alpha amplitude dictates more liberal versus conservative choices in confidence judgments, further modulated with incoming sensory evidence, and thus, having postperceptual effect on how we interpret our perceptual environment is yet to be addressed. However, we demonstrate that these oscillatory processes can be selectively modulated by noninvasive neurostimulation, offering a foundation to future translational neuroscience approaches and clinical applications.

STAR METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.01.003.

ACKNOWLEDGMENTS

F.D.G. is supported by the Ministero della Salute (SG-2018-12367527); A.A. is supported by the Fondazione del Monte di Bologna e Ravenna (339bis/2017), the Bial Foundation (347/18), and Ministero dell’Istruzione, dell’Università e della Ricerca (2017N7WCLP); and V.R. is supported by the Bial Foundation (204/18).

AUTHOR CONTRIBUTIONS


DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: August 18, 2021
Revised: November 30, 2021
Accepted: January 4, 2022
Published: January 27, 2022

REFERENCES


STAR METHODS

KEY RESOURCES TABLE

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SOFTWARE AND ALGORITHMS

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RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead contact, Vincenzo Romei (vincenzo.romei@unibo.it).

Materials availability
See the Key resources table for information about resources. This study did not generate new unique reagents.

Data and code availability
The datasets generated during this study have been made publicly available through the Open Science Framework: https://osf.io/e4bnj/. Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Experiment 1 Participants
Twenty-four healthy volunteers (12 women, 12 men; mean age ± SE = 23.2 ± 2.61) with normal or corrected vision participated in Experiment 1. Sample size was determined based on previous literature. Specifically, previous EEG studies on the role of pre-stimulus alpha in conscious perception considered a sample size between 10 and 26 participants. In addition, post-hoc power analysis (G-power 3.1) revealed that, for all significant ANOVA effects in our study, values of Power (1-β err prob) are >0.95. All participants were recruited at the Centre for Studies and Research in Cognitive Neuroscience in Cesena, Italy. The study was conducted in accordance with the Declaration of Helsinki. All participants gave written informed consent to participate in the study, which was approved by the bioethics committee of the University of Bologna.

Experiment 2 Participants
Fifty-one healthy volunteers (25 females, 26 males; mean age ± SE = 23.39 ± 0.36 years) took part in Experiment 2. Sample size was determined based on previous literature. Specifically, previous TMS studies on oscillatory entrainment considered a sample size between 7 and 17. In addition, post-hoc power analysis (G-power 3.1) revealed that, for all significant ANOVA effects in our study, values of Power (1-β err prob) are >0.95. All of the participants had normal or corrected-to-normal vision and met TMS safety criteria by self-report. All participants gave written informed consent before taking part in the study, which was conducted in
accordance with the Declaration of Helsinki and approved by the local ethics committee. Here, subjects were randomly assigned to one of three groups, with distinct stimulation protocols (see **method details** section): IAF-1Hz (group 1 = mean age 22.64 ± 0.52, nine females), IAF (group 2 = mean age 23.88 ± 0.52, eight females) and IAF+1Hz (group 3 = mean age 23.88 ± 0.77, eight females), each containing 17 participants.

**Experiment 3**

**Participants**

Seventeen healthy new volunteers (12 women, 5 men; mean age = 22.47, SE = 0.66) were recruited for Experiment 3.

**METHOD DETAILS**

**Experiment 1**

**Stimuli and task procedure**

Participants were comfortably seated in front of a CRT monitor (100Hz refresh rate) at a viewing distance of 57 cm. A PC running E-Prime software (Psychology Software Tools, Inc., USA) controlled stimulus presentation and responses registration. During the main experimental procedure (main task), each trial consisted of a **primary visual detection task**, in which participants responded to visual stimuli displayed on the computer screen, and a **secondary confidence task**, in which participants rated the level of confidence in their perception on a scale of 1 to 4, where 1 = no confidence at all; 2 = little confidence; 3 = moderate confidence; and 4 = high confidence. At the beginning of each trial, a white fixation cross was displayed on a grey background. The fixation cross was presented in the centre of the screen for 2000 ms and subtended a visual angle of 0.8°. Afterwards, an X (visual angle 2°) was created by rotating the fixation cross by 45 degrees. The cue appeared for a variable time period (time jitter between 2000 and 3000 ms), immediately followed by the primary task stimulus. The stimulus could appear with equal probability on the right or left visual field. These stimuli were presented at $4.1°/3.7°$ eccentricity (horizontal/vertical) in the lower part of the left visual field (LVF) or right visual field (RVF) for 60 ms. The primary task stimulus could be either a catch stimulus (50% of trials) or a target stimulus (50% of trials). Catch stimuli consisted of 8 x 8 black and white checkerboards (height = 4 cm; width = 4 cm; visual angle = 15.9°). Target stimuli consisted of the same checkerboard containing iso-luminant grey circles, which contrasted the black and white parts of the checkerboard. Participants were prompted to press the spacebar on the keyboard with their right index finger whenever they detected the circles embedded in the checkerboard. Primary response speed was not stressed over perceptual accuracy, but a time limit of 2000 ms was given. After this primary response, confidence ratings were collected. The Italian version of the question: “How confident are you about your percept?” was presented until participants rated their confidence. Confidence was rated on a 4-points Likert scale, from “no confidence at all” to “high confidence”, and was reported by pressing the corresponding number on the keyboard with the left index finger. Notably, here the confidence rating reflects a participant’s level of subjective certainty in having correctly perceived the stimulus. After rating their confidence, a new trial started with the presentation of a new fixation cross. The main task consisted of 5 blocks with 60 trials per block (total trial number = 300) and lasted on average 90 min.

**Titration session**

A titration session was run before the main experimental session in order to set stimuli contrast ratios corresponding to each individual’s 50% perceptual threshold. Iso-luminant circles of 8 different contrast ratios (RGB contrasts on black/white background: 28/227, 32/223, 36/219, 40/215, 44/211, 48/207 and 100/155) were presented together with catch trials (checkerboards without iso-luminant circles).


To account for individual biases among participants in their response to catch trials, a false alarm rate was considered, together with target stimuli of different contrast for the calculation of the sigmoid function. For each iso-luminant contrast, individual performance was then entered to calculate the sigmoid function.
Data were analyzed using the following formula to calculate the threshold value ($y$):

$$y = \frac{100}{1 + e^{-\frac{x}{c}}}$$

Where $x$ is the contrast value, $c$ is the inflection point of the curve and $d$ is the slope of the sigmoid.

The corresponding inflection point was selected as the bias-adjusted threshold, which was used for stimulus presentation during the experiment. In Experiment 1, detection performance threshold during the main task ($M = 56.9\%$, $SE = 3.69\%$) was not statistically different from the bias-adjusted threshold ($M = 51.58\%$, $SE = 0.48\%$) calculated during the titration session, ($t(24) = 1.68$, $p = .11$, $d = 0.34$). Across participants, the selected luminance contrast ratios during the main task ranged between 20/235 and 50/205 RGB points ($M = 32/223$, $SE = 12$).

**Experiment 2**

Both Experiment 2 and Experiment 3 implemented a rhythmic-TMS entrainment protocol with concurrent EEG recording. The timing of rhythmic-TMS pulses differed between the two experiments.

**Stimuli and task procedure**

Stimuli and tasks in Experiment 2 were the same as those described for Experiment 1, with the main difference being the active manipulation of alpha activity via an entrainment protocol.

Entrainment of the intrinsic oscillatory alpha activity was achieved using rhythmic transcranial magnetic stimulation (rhythmic-TMS). Specifically, pre-stimulus alpha activity was fine-tuned relative to individual alpha frequency using rhythmic five-pulse TMS bursts in which the time lag between pulses was manipulated depending on the group. In order to induce changes in the alpha-frequency cycle length, rhythmic-TMS was applied at a slower or faster pace, relative to a participant’s individual alpha-frequency. To selectively modulate alpha amplitude, the frequency of the rhythmic-TMS pulse trains was matched to the intrinsic individual alpha-frequency of the participant, thus enhancing the synchronization of neural firing and phase alignment without influencing the speed of alpha activity. In this way, rhythmic-TMS pulse trains could occur at three different frequencies: at the individual alpha-frequency of the participant to manipulate pre-stimulus alpha amplitude (IAF group); at 1Hz lower than the individual alpha-frequency (IAF-1Hz group) to slow-down pre-stimulus alpha-frequency; or at 1Hz higher than the individual alpha-frequency (IAF+1Hz group) to speed-up pre-stimulus alpha-frequency. In all groups, the last TMS-pulse coincided with the stimulus appearance.

Biphasic stimulation was applied using a Magstim Rapid Transcranial Magnetic Stimulator via a 70mm figure-of-eight coil (Magstim Company, UK) of maximum field strength ~1.5T. As systematic differences in visual cortex excitability do not seem to be present between the hemispheres, TMS bursts were delivered only to the right occipital site (at O2 electrode position), with the coil surface tangent to the scalp, and the handle oriented perpendicular to the medial plane of the subjects head (latero-medial current direction). Moreover, pulse intensity was kept fixed at 60% of the maximum stimulator output (MSO), roughly corresponding to previously reported phosphenes thresholds. No subject reported to have perceived phosphenes during the execution of the task. Within-subject sham control stimulation was implemented in order to account for any non-specific rhythmic-TMS effects. To do so, a modified coil was used that provided enough distance from the scalp to ensure the absence of stimulation, while at the same time maintaining coil position, as well as tactile and acoustic sensations. Each participant underwent three consecutives rhythmic-TMS and sham blocks (resulting in a total of 900 active rhythmic-TMS pulses), whereas rhythmic-TMS/sham stimulation block order was randomized. Therefore, the experimental session consisted of 6 blocks with 60 trials per block (total trial number = 360) (see also Experiment 1), with short breaks between the blocks (overall average task duration of 50 minutes). The rhythmic-TMS design was in line with current safety guidelines.

**Titration session**

Titration was run as for Experiment 1. Additionally, in the second experiment, during the titration session, individual alpha peak frequency (defined as the maximum local power in the alpha-frequency range) was determined. A total of six minutes resting-state EEG (three minutes with eye closed and three minutes with eyes open, and with gaze on a fixation cross on the screen) was recorded from 8 Ag/AgCl parieto-occipital electrodes (O1,P3,PO3,P07; O2,P4,PO4, PO8). Individual alpha-frequency peak was calculated from the power spectra of the eyes open condition, applying a Fast Fourier Transformation. In line with Experiment 1 (showing a local alpha power maxima over O2) and previous studies, alpha-frequency was calculated from the O2 electrode, over which rhythmic-TMS was subsequently applied (see above). The identified individual alpha-frequency was used to calibrate rhythmic-TMS frequency.

**Experiment 3**

**Stimuli and task procedure**

The stimuli and task for Experiment 3 were the same as those used for Experiment 2, the main difference being the timing of the manipulation of alpha activity via an entrainment protocol.

Specifically, Experiment 3 aimed to selectively enhance post-stimulus alpha-amplitude, prior to the confidence prompt. As such, only one entrainment protocol was applied (i.e. stimulation at the individual alpha-frequency). While in Experiment 2, the final pulse of the rhythmic-TMS-train coincided with stimulus onset, in Experiment 3, the final rhythmic-TMS pulse coincided with the onset of the confidence prompt.

Stimulation site, coil orientation, stimulation intensity, control conditions and number of pulses were the same as those used in Experiment 2.
**Titration session**

The titration session was conducted as in Experiment 2.

**QUANTIFICATION AND STATISTICAL ANALYSIS**

**Experiment 1**

**Psychophysiological recording—paradigm and acquisition**

EEG data were collected during the main task in Experiment 1 from 64 Ag/AgCl electrodes (Fp1,Fp2,AF3,AF4,AF7,AF8,F1,F2, F3,F4,F7,F8,FC1,FC2,FC3,FC4,FC5,FC6,FT7,FT8,C1,C2,C3,C4,C5,C6,T7,T8,CP1,CP2,CP3,CP4,CP5,CP6,TP7,TP8,P1,P2,P3,P4, P5,P6,P7,P8,PO3,PO4,PO7,PO8,O1,O2,Fpz,AFz,Fz,FCz,Cz,CPz,Pz,POz,Oz) and from the right mastoid with BrainVision recorder software (Brain Products, Munich, Germany). The left mastoid was used as reference, and the ground electrode was placed on the right cheek. The electrooculogram (EOG) was recorded from above and below the left eye and from the outer canthi of both eyes. EEG and EOG were recorded with a band-pass filter of 0.01–100Hz, at a sampling rate of 1000Hz, which was re-sampled to 500Hz offline. The impedance of all electrodes was kept below 10kΩ. EEG data were pre-analyzed using custom made routines in MatLab R2013b (The Mathworks, Natick, MA, USA). EEG data were re-referenced off-line to the average of all electrodes and filtered with a 0.5–30Hz pass-band. Epochs were extracted stimulus-locked from -1500ms to 2500ms. Artefact-contaminated epochs were excluded using the pop_autorej function in EEGLAB v13.0.1, which first excludes trials with voltage fluctuations larger than 1000 μV, and then excludes trials with data values outside five standard deviations (mean=9.7% SE=2.9% of trials removed). Subsequently, EOG artefacts were corrected by a procedure based on a linear regression method (lms_regression function in MatLab R2013b). Because perceptually relevant, pre-stimulus alpha activity shows hemispheric lateralization, relative to upcoming stimulus location, we recoded electrode positions as contralateral versus ipsilateral to the hemifield of stimulus presentation (resulting in all contralateral activity being on one side, which was conventionally defined to be the right), i.e. for RVF-stimulus epochs, data from the contralateral (left) electrodes were copied and flipped to right-sided electrodes, electrodes on the midline were not flipped or recoded.

In order to identify the individual alpha-frequency peak during the task, data epochs in the cue-stimulus period (i.e. pre-stimulus alpha from -1000ms to stimulus presentations, baseline between -1500 and -1000ms) were analyzed with a fast Fourier transformation (MatLab function spectroco, frequency resolution: 0.166Hz). Power was calculated separately for each subject and condition and was normalized by z-score decibel (dB = 10*log10[-power/baseline]) transformation at each frequency. Individual alpha-frequency was defined as the local maximum power within the frequency range 7-13Hz (i.e. alpha peak). Each subject showed a clear peak within this alpha range. However, a peak in the alpha-band was not present at all electrodes. For this reason, power spectra on all parietal-occipital electrodes were visually inspected. Then, the contralateral electrode was selected for analyses where alpha oscillation showed a clear peak. Homologous electrodes were selected for the analyses in the ipsilateral hemisphere. This procedure identified the following subset of parieto-occipital electrodes that were used separately for each subject and condition to identify alpha-frequency in the cue-stimulus period: contralateral electrodes (P8,PO8,PO4,O2), and ipsilateral electrodes (P7,PO7,PO3,O1). Importantly, most of the participants (n = 15) showed maximum power over electrode O2.

The amplitude of alpha oscillations was calculated by time-frequency analyses of data epoched from 2000ms before to 2000ms after the stimulus onset. Long epochs prevent edge artefacts from contaminating time frequency power in the time windows of interest. Spectral EEG activity was assessed by time-frequency decomposition using a complex sinusoidal wavelet convolution procedure (between 2 and 25 cycles per wavelet, linearly increasing across 50 linear-spaced frequencies from 2.0Hz to 50.0Hz) with the newtimef function from EEGLAB v13.0.1, and custom routines in MatLab. The resulting power was normalized by decibel (dB = 10*log10[-power/baseline]) transformation at each frequency, using a single trial baseline between -1000 and -500 preceding stimulus onset. This baseline window was used to increase the signal-to-noise ratio during the baseline period and is frequently applied in time frequency analyses. This procedure was applied separately for each subject and condition. Mean alpha (7-13Hz) amplitude was computed separately for each condition in the cue-stimulus interval (-500 to 0ms) and in the post-stimulus interval (0 to 900ms), which corresponds to the pre-confidence prompt time period. In order to identify electrode clusters for the analyses of alpha-amplitude, we used the same procedure as for alpha-frequency. For alpha-amplitude, the following subsets of posterior contralateral (P2,P4,P8,PO4,PO8,O2) and ipsilateral (P1,P3,P7,PO7,PO3,O1) electrodes were used for the analyses. Importantly, as for alpha-frequency, most of the participants (n=18) showed maximum alpha-amplitude over electrode O2.

**Statistical analyses**

First, trials were sorted according to objective accuracy (i.e. into correct and error trials). Correct trials consisted of correctly detected target trials (i.e. hits, where participants pressed the spacebar after a target trial) and correctly detected catch trials (i.e. correct rejections, where participants did not press the spacebar after a catch trial). Accordingly, error trials consisted of misses after target trials and false alarms after catch trials. Then we compared participants with high vs low perceptual sensitivity. Perceptual sensitivity was estimated using the d’ measure. In signal detection theory (SDT), d’ reflects standardized measure of discrimination abilities between the signal and the noise (type I sensitivity). d’ was calculated as d’ = z(H) – z(FA), where z represents the z-scores of Hit rate (i.e. H, the probability of correct reactions on target trials) and false alarms (i.e. FA, the probability of incorrect reactions on catch trials).

Next, we focused on subjective confidence levels during correct trials (i.e. hits and correct rejections). In order to compare confident vs. non-confident responses, we aggregated high confident responses and low confident responses. In this way, correct trials...
were divided in high confident (i.e. with a confidence rating of 3 or 4) and low confident (i.e. with a confidence rating of 1 or 2) trials. Then, we compared participants showing high vs low confidence or metacognitive performance. For confidence analyses, the mean value of the confidence ratings was calculated for each participant. Instead, metacognitive performance was quantified using the computational method proposed by Maniscalco & Lau. This method quantifies the efficacy of confidence ratings to discriminate between correct and erroneous responses in a SDT model. The model accounts for the variance in task performance to compute metacognitive sensitivity (type II sensitivity) on subjective confidence rating. This method, previously described in detail and validated, can give a metric (termed meta-d') for metacognitive abilities.

Briefly, the central idea is to link type I and type II SDT models to compute the observed type II sensitivity. meta-d' estimates the values, which maximize the fit between the observed type II data and the parameter values of the d' type I SDT model. Here, meta-d' was calculated with the function fit_meta_d_SSE in MatLab. This function minimizes the sum of squared errors and estimates meta-d' using observed type II data and the empirical type I criterion c. In this way, meta-d' estimates, for instance, the relative likelihood to report a high confidence rating after a correct response. Higher values of meta-d' correspond to participants having better metacognitive abilities.

Within participants EEG analyses were performed for objective accuracy and subjective confidence. For Objective Accuracy, we compared alpha activity (both frequency and amplitude) in 2x2 repeated measures ANOVAs with the factors ACCURACY (correct and incorrect) and HEMISPHERE (contralateral and ipsilateral). For Subjective Confidence, analyses were performed on correct trials. Alpha activity was analyzed for the factor CONFIDENCE (high and low confidence) and for the factor HEMISPHERES (contralateral and ipsilateral) in 2x2 repeated measures ANOVAs. Differences between conditions were tested by one or two-tailed t-tests (planned comparisons).

Between participants EEG analyses were performed on perceptual sensitivity and metacognitive performance. For perceptual sensitivity analyses, we divided participants in two numerically equivalent groups using the median split of the d' scores (high vs low d'). As for perceptual sensitivity, we also conducted between-group analysis, by dividing participants in two numerically equivalent groups (high vs low meta d' scores) on a median split basis of the meta-d' scores (i.e. metacognitive performance). Differences between groups were tested by one- or two-tailed independent samples t-tests (planned comparisons).

Pre-stimulus IAF and resting-state IAF
As we have used resting IAF to target pre-stimulus activity in experiments 2 and 3 (see results sections), we checked for any potential difference between resting-state IAF and pre-stimulus IAF in Experiment 1 to ensure adequacy of our approach, with the working hypothesis that no significant differences should be observed. In this analysis, resting-state IAF was defined as the maximum local power in the alpha-frequency range during the resting state over a cluster of posterior electrodes (O1,P1,P3,P5,P7,Pz,POz,Oz, PO3,PO7; O2,P2,P4,P6,P8,PO4,PO8), while pre-stimulus IAF was calculated in the same electrode cluster across conditions in a time window between -1000ms and stimulus presentation. The analysis was performed on 22 out of 24 participants as resting EEG was not available for 2 participants. As expected, the two-tailed paired samples t-test showed no differences (t(21) = 0.05, p = .968, d = .019) between resting state IAF (M = 10.81Hz; SE = 0.21Hz) and pre-stimulus IAF (M = 10.83Hz; SE = 0.37Hz). Importantly, these results demonstrate that resting-state IAF and pre-stimulus IAF are comparable within group.

Experiment 2
EEG recordings – acquisition and processing
EEG data were collected for Experiment 2 as for Experiment 1. However, in Experiment 2, a rhythmic-TMS pulse train was applied during EEG recording. The resulting rhythmic-TMS artefacts were identified and removed using an open-source EEGlab extension, the TMS-EEG signal analyzer (TESA). First, EEG data were epoched around stimulus onset (between -1500ms and 2500ms for Experiment 2 and between -1000ms and 2000ms for Experiment 3, due to differences in stimulation timing) and the linear trend from the obtained epochs was removed. Then rhythmic-TMS pulse artefact and peaks of rhythmic-TMS-evoked scalp muscle activities were removed (-10ms +10ms) and cubic interpolation was performed prior to down-sampling the data (from 5000Hz to 1000Hz). Interpolated data was again removed prior to Individual Component Analysis (ICA). Specifically, a fastICA algorithm was used (pop_tesa_fastica function: http://research.ics.aalto.fi/ica/fastica/code/dlcode.shtml) to identify individual components representing artefacts, along with automatic component classification (pop_tesa_compselect function), where each component was subsequently manually checked and reclassified when necessary. In this first round of ICA, only components with large amplitude artefacts, such as rhythmic-TMS-evoked scalp muscle artefacts, were eliminated. Data were again interpolated prior to applying pass-band (between 1 and 100Hz) and stop-band (between 48 and 52Hz) Butterworth filters. Subsequently interpolated data were again removed prior to the second round of ICA, in order to remove all other artefacts, such as blinks, eye movement, persistent muscle activity and electrode noise. Then, rhythmic-TMS-pulse period was interpolated and data was re-referenced to the average of all electrodes. Finally, single trials were visually inspected and those containing residual rhythmic-TMS artefact were removed. The described rhythmic-TMS artefact removal procedure was applied to all EEG data, both for active rhythmic-TMS and sham stimulations. On average, approximately one third of all epochs were removed (M = 34.31%, SE = 1.72%) (remaining epochs mean = 236.5 epochs, SE = 6.19). A graphical explanation of the artefact correction procedure is reported in the supplementary information (see Figure S3).

Alpha-frequency and alpha-amplitude were identified in a similar manner as per Experiment 1. Alpha-frequency was defined as the local maximum power within the frequency 7-13Hz range in a pre-stimulus period (-650ms to stimulus presentation). Accordingly, pre-stimulus alpha-amplitude was calculated in the time frequency data (as for Experiment 1). The time window of analyses...
corresponded to stimulation period for both alpha-frequency and -amplitude. Near-stimulation parieto-occipital electrodes in the right hemisphere (PO4,PO8,O2), along with analogous electrodes in the left hemisphere (PO3,PO7,O1) were used for all of the analyses.

**Statistical analyses (behavioral data)**

Behavioral data were analyzed separately for perceptual sensitivity (d’ score) and for confidence (mean of confidence ratings) and metacognitive performance (meta d’ score).

All scores were compared between the two HEMIFIELDS (left and right) and two STIMULATION types (active rhythmic-TMS and sham) in three GROUPs of participants (IAF±1Hz, IAF), in 2x2x3 repeated measures mixed-model ANOVAs.

**Statistical analyses (EEG data)**

Electrophysiological data were analyzed separately for pre-stimulus alpha-amplitude and alpha-frequency. Therefore, both parameters of alpha activity were compared between the two HEMISPHERES (left and right parieto-occipital cluster) and the two STIMULATION types (active rhythmic-TMS and sham) in three GROUPs of participants in 2x2x3 repeated measures mixed-model ANOVAs. Differences between conditions were tested by two-tailed t-test (planned comparisons).

Finally, the association between rhythmic-TMS-evoked differences in alpha-frequency in the stimulated (right) hemisphere (computed as a difference in alpha-frequency between active rhythmic-TMS and sham stimulation conditions) and differences in perceptual sensitivity in the opposite (left) hemispace (computed as a difference in d’ score between active rhythmic-TMS and sham stimulation conditions) was explored via linear regression.

**Experiment 3**

**EEG recordings – acquisition and processing**

EEG data were recorded and alpha-frequency and alpha-amplitude identified as in Experiments 1 and 2, with the only difference being that the analysis window was moved to a time window preceding the confidence prompt (850ms to 1500ms after stimulus presentation, which corresponded to -650ms prior to the confidence prompt).

**Statistical analyses (behavioral data)**

Behavioral data were analyzed separately for perceptual sensitivity (d’ score) and for confidence (mean of confidence ratings) and metacognitive performance (meta d’ score). All scores were compared for the two HEMIFIELDS (left and right) and between different STIMULATION types (active rhythmic-TMS and sham) in a 2x2 repeated measures ANOVA.

**Statistical analyses (EEG data)**

Electrophysiological data were analyzed separately for alpha-amplitude and alpha-frequency. Moreover, differences in alpha-amplitude and alpha-frequency were again compared between the two HEMISPHERES (left and right) and between STIMULATION types (active rhythmic-TMS and sham) in a 2x2 repeated measures ANOVA. Differences between conditions were tested by two-tailed t-test (planned comparisons).

Finally, a linear regression model was used to determine whether rhythmic-TMS-evoked differences in alpha-amplitude in the stimulated (right) hemisphere (computed as a difference in alpha-amplitude between active rhythmic-TMS and sham stimulation conditions) can predict differences in confidence levels in the opposite (left) hemispace (computed as a difference in meta d’ scores between active rhythmic-TMS and sham stimulation conditions).