Distributed attention is implemented through theta-rhythmic gamma modulation

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Highlights

- Two stimuli’s gamma responses are subtracted (LGA) to reveal attentional biases.
- The 4 Hz phase of LGA before one of the stimuli dims predicts detection accuracy.
- The magnitude of this accuracy modulation is 14.5% of the average accuracy.
- The 4 Hz modulation of gamma responses was evident throughout the attention period.

In Brief

Attentional capture to one of two stimuli leads to performance fluctuations suggesting that attention samples each stimulus at 4 Hz, in alternation. Landau et al. use MEG to record the two stimuli’s gamma responses. A 4 Hz gamma-response alternation predicts behavioral accuracy and thereby reveals that attentional sampling is continuously ongoing.
Distributed attention is implemented through theta-rhythmic gamma modulation

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SUMMARY

When subjects monitor a single location, visual target detection depends on the pre-target phase of an ~8 Hz brain rhythm [1, 2]. When multiple locations are monitored, performance decrements suggest a division of the 8 Hz rhythm over the number of locations [3], indicating that different locations are sequentially sampled. Indeed, when subjects monitor two locations, performance benefits alternate at a 4 Hz rhythm [4]. These performance alternations were revealed after a reset of attention to one location. Although resets are common and important events for attention [5], it is unknown, whether in the absence of resets, ongoing attention samples stimuli in alternation. Here, we examined whether spatially specific attentional sampling can be revealed by ongoing pre-target brain rhythms. Visually induced gamma-band activity plays a role in spatial attention. Therefore, we hypothesized that performance on two simultaneously monitored stimuli can be predicted by a 4 Hz modulation of gamma-band activity. Brain rhythms were assessed with magnetoencephalography (MEG), while subjects monitored bilateral grating stimuli for a unilateral target event. The corresponding contralateral gamma-band responses were subtracted from each other to isolate spatially selective, target-related fluctuations. The resulting lateralized-gamma activity (LGA) showed opposite pre-target 4 Hz phases for detected versus missed targets. The 4 Hz phase of pre-target LGA accounted for a 16% modulation in performance. These findings suggest that spatial attention is a theta-rhythmic sampling process that is continuously ongoing, with each sampling cycle implemented through gamma-band synchrony.

RESULTS AND DISCUSSION

Attention research often investigates performance, or neural responses, to a stimulus that is behaviorally relevant, as compared to responses to irrelevant stimuli [6]. Studies over the past decades produced several insights and characterized neural as well as behavioral signatures of attentional deployment [7–9]. Recently, evidence is accumulating that in the case of a single focus of attention, attentional benefits are not sustained but rather entail a periodic temporal structure. For example Busch, Dubois and VanRullen [1] have shown that the phase of a pre-stimulus 8 Hz EEG oscillation can predict the ability of an observer to correctly identify an upcoming stimulus at a known location. The ability to predict behavior from a rhythmic neural process suggests that attention may directly entail a sampling mechanism rather than a resource that can be continuously deployed. In order to incorporate this idea into physiological and cognitive models of attention, it is pivotal to examine whether such rhythmic modulation of perception is a spatially selective process, consistent with previous characterizations of spatial attention (e.g.[5]), as opposed to a spatially-unspecific effect. This can be achieved by examining the temporal structure of attention when more than one location, or stimulus, is behaviorally relevant. Previous psychophysical studies [4, 10] used a cue to reset attention to one of two objects and found that subsequently, attention sampled each object sequentially at 4 Hz. This finding is consistent with an 8 Hz sampling mechanism that is distributed over two objects.
Figure 1: Schematic of the attentional sampling hypothesis and experimental approaches testing it. (A) Two alternative accounts of a previous psychophysical experiment, motivating the current MEG experiment, which is illustrated in (B). The psychophysical experiment utilized a reset event (black vertical line and four dots surrounding the circle) to capture attention to one of two monitored stimuli (L: left; R: right). After the reset, 4 Hz fluctuations in behavioral performance were observed and suggested that attentional sampling alternated between the reset-cued, and the opposite, stimulus. In one account (upper half, option 1), the observed sampling exists already before the reset and is merely rendered visible in behavior due to the reset. In an alternative account (lower half, option 2), no attentional sampling is present until the reset event captures attention to one stimulus and perturbs an otherwise non-rhythmic process. (B) To determine whether attentional sampling occurs in the absence of a reset event, the neuronal representation of the two stimuli has to be measured physiologically. MEG allows for the measurement of visual gamma responses to each visual field and computation of the lateralized gamma activity (LGA = green lines) preceding the target event. LGA is defined as the difference between the ipsilateral gamma-band envelope (blue lines) and the contralateral gamma-band envelope (red lines). LGA for hit and miss trials (solid and dashed lines, respectively) was computed, and phase consistency based on all hit-miss trial combinations was calculated. Gray-filled circles represent moments in an ongoing gamma fluctuation during which a target event occurs on the ‘R’ stimulus. Such events would be the ones to which the LGA response is aligned to. RVF and LVF, Right and Left visual field respectively. See also Figure S2
resulting in the measured 4 Hz per object. Importantly, given the alternating (i.e. serial) nature of performance benefits between the two objects, this finding provided evidence that such sampling is indeed a spatially specific process indicative of a mechanism of selective attention rather than of non-specific vigilance.

A reset event allows to quantify attentional benefits as a function of time following the reset. In the previous psychophysical studies, the observed rhythmic fluctuations in performance were interpreted as an ongoing sampling mechanism that is merely revealed through the reset (Figure 1, option 1). It is possible, however, that the reset event did not only reset an ongoing sampling rhythm but rather introduced such temporal structure into performance that otherwise was either non-sampling (Figure 1, option 2) or non-alternating (option not illustrated). In order to disambiguate these possibilities and in order to investigate the neural fate of stimuli presented in such distributed attention conditions, we examined visual responses measured with magnetoencephalography (MEG). We tested a concrete physiological prediction that follows from the notion of ongoing attentional sampling: Attentional sampling, i.e. alternating performance enhancements, should be optimally captured by the difference between two neuronal representations corresponding to the two stimuli. To derive such a stimulus-specific response metric, we used the stimulus-induced gamma-band power time course. Using this signal is neurophysiologically motivated and also has methodological utility. Methodologically, to derive a stimulus-specific response difference, we cannot subtract the raw EEG or MEG signal (neither at sensor nor source level), because the phase of such signals is always ambiguous between a given phase and its 180° counterpart (as also mentioned in [11]). In contrast, the stimulus-induced gamma-band power time course can be subtracted between different sources (representing different stimuli), because it is a rectified signal for which absolute phase is interpretable. Importantly, from a neurophysiological perspective, gamma is closely linked to stimulus processing and is enhanced by attentional selection [12], making it a functionally relevant processing signal when investigating the consequences of distributed spatial attention.

Twenty-two subjects participated in the experiment after providing informed consent, with the approval of the local ethics committee. In each trial, subjects fixated on a central dot and monitored two stationary gratings for a small, localized contrast decrement (“target”) that occurred at one unpredictable moment per trial (up to 4 s after stimulus onset) and with equal probability within either grating. The two gratings were placed in the two visual hemifields to induce responses primarily in the respective contralateral hemispheres, such that the difference between neuronal stimulus representations could be calculated as the difference between corresponding source locations in the two hemispheres. This difference calculation eliminated dynamics due to stimulation, task structure, or intrinsic global fluctuations, and emphasized momentary biases in the processing of one versus the other stimulus. Based on the previous studies discussed above, we hypothesized that these momentary biases account for attentional sampling at 4 Hz, and therefore, that the 4 Hz phase of this hemisphere-difference predicts detection accuracy. Therefore, we analyzed the 0.5 s epoch preceding the unilateral target event (contrast decrement) occurring within one of the two stimuli. Source-projected gamma-band activity contralateral to the target minus the homologous ipsilateral activity was referred to as lateralized gamma-band activity (LGA). We tested for all source locations (1 cm grid) and all frequencies (2-20 Hz), whether the phase of the LGA was in anti-phase preceding hits versus misses.

We considered all possible pairings of hit with miss trials. For each hit-miss trial pair, we calculated per frequency the cosine of the phase difference and subsequently averaged across all hit-miss trial pairs. The resulting phase consistency metric (PCM) is an unbiased quantity (for a discussion on bias in phase consistency estimation see [13]) which was determined separately per source location and frequency. Positive PCM values indicate that hits and misses are preceded by the same phase and negative values are an indication of opposite phase. Statistical significance was determined with a permutation test that implemented a non-parametric
version of a two-sided random-effect test with multiple comparison correction across source locations and frequencies (see Supplemental Experimental Procedures for details). Across sources and frequencies, we found one significant, negative cluster at 4 Hz consisting of 26 adjacent sources spanning calcarine sulcus, lingual and precuneus gyri (Figure 2). The cluster lies within the region for which source-projected gamma-band activity was enhanced by visual stimulation as compared to pre-stimulus baseline (Figure S1). The gamma-peak frequency in the cluster corresponded closely to the gamma-peak frequency used for LGA calculation (Table S1), which we had derived from the sources with maximal visually induced gamma-band activity. The negative sign of the cluster indicates that the phase relationship between hit- and miss-trials was consistently opposite. There were no further significant clusters at 4 Hz. Importantly, there were also no further significant clusters for any other frequencies up to 20 Hz, which was the highest frequency tested. Higher LGA modulation frequencies would require fluctuation in gamma power on a faster time scale than we could capture with the three-gamma-cycle window used here.

We directly quantified the 4 Hz phase relation of the LGA between hit and miss trials and confirmed that they were significantly non-uniform (Rayleigh test for non-uniformity across subjects; p<1.4e-16), with a mean phase relationship of -177 degrees, and significantly different from 0 degree (p<0.01).

To further characterize the phase relationship between LGA fluctuations preceding hits versus misses, we averaged PCM values across all sources within the significant cluster, separately for all frequencies below 12 Hz (Figure 3). This analysis revealed a significant, negative peak of the PCM at 4 Hz. While the above analysis across sources and frequencies already suggests this result, Figure 3 further illustrates the spectral specificity in agreement with our earlier psychophysical findings.
demonstrating a 4 Hz sampling for two simultaneously monitored stimuli [4]. Note that the small absolute values of the PCM are difficult to interpret due to the fact that those reflect the averaging of all possible pairs of individual hit and miss trials. The functional relevance of those PCM values can be explored by investigating the modulation depth in behavioral performance accounted for by the 4 Hz LGA phase.

Therefore, we tested how behavioral performance fluctuates as a function of 4 Hz phase of the pre-target LGA. This analysis used the same LGA phases as Figure 2, but only from the sources within the significant cluster of Figure 2. To this end, we sorted the data into 11 non-overlapping bins. We calculated a circular-linear correlation between detection performance and phase, separately per subject and source location, and subsequently averaged across source locations to obtain one correlation per subject. Across subjects, correlation values were significantly higher compared to a randomization distribution of circular-linear correlations [t(21) = 10.6, p = 6.82e-10]. At the level of individual subjects, the correlation was significant in nineteen of twenty-two participants. Given that accuracy was correlated with LGA 4 Hz phase, we proceeded to investigate the precise form of this dependence. Similar to previous work [1], we first determined the 4 Hz LGA phase associated with peak performance per subject and source, aligned phases to this optimal phase, and then calculated behavioral accuracy for all 11 phase bins (Figure 4). Although this alignment fixes the peak performance value to zero phase, it does not constrain the values for the other, non-overlapping phase bins. The resulting accuracy-by-phase plot, excluding the performance value at zero-phase, was fitted by a sine wave. The fitting procedure was performed separately for each participant, using a linear regression. This procedure quantified the amplitude of each individual participant’s fit and revealed that the pre-target 4 Hz LGA phase modulates accuracy in a sinusoidal way. The absolute modulation depth was 7.6%. Given an average accuracy of 52.4%, this corresponds to a relative modulation of 14.5%.

In order to test for significance, we used the distribution of fitted sinusoidal amplitudes across subjects to generate a randomization distribution. The observed amplitude was significantly larger than the randomization mean amplitude (p<0.001). The average r-value for the binned data was 0.67 corresponding to an r-squared of 0.44. Consistent with that, performance differed significantly between the peak-performance phase bin and the opposite phase bin (t(21) = 7.27 p = 3.7e-07).

These results suggest that attentional selection, implemented through gamma-band synchronization, is continuously sampling the two stimuli at 4 Hz each. The pattern of results suggests that the theta phase modulates gamma power throughout stimulus presentation. Similar theta-gamma coupling has been demonstrated in several previous studies, but typically without a clear link to theta-rhythmic modulation in behavioral performance. To relate our findings to previous studies, we quantified the modulation of gamma power by theta phase throughout the trial and without reference to the target event and subsequent behavioral performance. This analysis demonstrated a peak at 4 Hz (t(42) = 2.165, p<0.05) (Figure S2).

In summary, we show that a 4 Hz rhythm is present in the LGA of early and intermediate visual areas during distributed spatial attention, analogous to the 4 Hz fluctuations in behavioral performance [4]. Importantly, the spontaneously ongoing 4 Hz fluctuation of LGA predicted performance on a temporally unpredictable event in the absence of a temporal reset. Thus, the present results strongly suggest that attention is continuously sampling attended locations at an 8 Hz rhythm such that each of two locations is sampled at a 4 Hz rhythm.

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Correspondingly, the 4 Hz modulation of gamma was evident throughout the sustained attention period.

Although there was no external resetting event, it is possible that there were internally generated visual resetting events like microsaccades (MSs). MSs have been shown to be partially predicted by the phase of a theta rhythm in primate visual cortex [14]. Furthermore, MSs have been shown to influence detection performance [15]. A rhythmic displacement of eye position might produce a systematic modulation in detection performance as well as an accompanying gamma-band modulation.

To investigate the relationship of eye movements to the sampling dynamic we report here, as well as to rule out such accounts for our data, we analyzed the eye-position time series acquired together with the MEG data. As can be seen in Figure S3, there was no systematic eye-position displacement that would match a 4 Hz relationship between visual processing and detection performance. Additionally, we analyzed the eye-position data in a way that mirrored the analysis of LGA as closely as possible (see Supplementary Methods), and this confirmed that hits versus misses were not preceded by rhythmic eye movement components. Therefore, the modulation we found in the LGA, which predicted behavior, was an ongoing brain process, rather than merely reflecting the rhythmic displacement of eye position.

The literature linking performance to pre-stimulus theta phase in non-invasive physiology has typically investigated perceptual events or detection performance at a single location (e.g., [1, 16, 17]). Here we document, to the best of our knowledge, for the first time that the ongoing 8 Hz rhythmic gamma modulation we found in the LGA could mirror the analysis of LGA as closely as possible (see Supplementary Methods), and this confirmed that hits versus misses were not preceded by rhythmic eye movement components. Therefore, the modulation we found in the LGA, which predicted behavior, was an ongoing brain process, rather than merely reflecting the rhythmic displacement of eye position.

In a previous neurophysiological study, neurons in the inferotemporal (IT) cortex, which represent almost exclusively the attended stimulus [21], showed pronounced firing rate modulations in response to stimulus onsets [22]. When a new stimulus was added to an already existing one, the respective stimulus representations alternated. The representation of each stimulus fluctuated at a 4 Hz rhythm [22]. Similarly, a 4 Hz rhythm has been shown to modulate gamma-band activity in numerous brain areas [6, 23–25]. Finally, gamma-band synchronization has been shown to subserve attentional selection [6, 12, 26]. Attention to a visual stimulus results in enhanced local and inter-areal synchronization among the respective neurons. The synthesis of these observations led us to suggest that the ongoing theta-rhythmic modulation of gamma-band activity implements an ongoing attentional sampling. In the present study, we use a given hemisphere’s gamma-band activity as a neuronal representation of the contralateral stimulus, analogous to the stimulus preferences of the IT neurons reported in [22]. Whereas in that study, stimulus onsets likely reset attention, we removed such reset events, and rather based the analysis on contrasting hit versus miss trials in order to study ongoing attentional sampling.

Although we used gamma-band activity mainly as a proxy for local neuronal processing, local gamma-band activity can lead to inter-areal gamma-band synchronization, which is an important candidate mechanism for inter-areal communication, according
to the communication-through-coherence (CTC) hypothesis [6, 12]. For example, gamma-band synchronization between visual areas V1 and V4 during an attention task is strongly modulated by theta phase [6]. Thus, the finding of LGA theta phase predicting behavioral performance suggests that CTC mechanisms might be employed at a theta rhythm. Future studies could directly investigate whether theta-rhythmic modulations of inter-areal synchronization account for behavior as predicted if they indeed constitute attentional sampling.

**EXPERIMENTAL PROCEDURES**

A description of the essential experimental and data analytical procedures is presented in the Results. A complete description can be found in the Supplemental Experimental Procedures.

**AUTHOR CONTRIBUTIONS**

Conceptualization, ANL and PF; Methodology, ANL and PF; Investigation, ANL and HMS; Analysis, ANL, SVP and PF; Writing, ANL and PF.

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**REFERENCES**

Figure S2

Pairwise Phase Consistency (PPC)

Frequency (Hz)
Figure S3

A. Left target events

B. Right target events

Horizontal eye position (degree visual angle)

Time relative to target event (s)

Hit trials
Miss trials
Supplemental Figure Legends:

**Figure S1 related to main Figure 2:** Spatial distribution of visually induced gamma-band power changes.

**Figure S2 related to main Figure 1:** Cross frequency correlation between the ongoing gamma power fluctuation and phase at different lower frequencies (x-axis). The gray line represents the result of repeating the same analysis after random shuffling of trials from which gamma-power time courses and lower-frequency phase time courses, respectively, were taken.

**Figure S3 related to main Figure 3:** Averaged horizontal eye position data for left and right target events. When traces are separated for hit (purple) versus miss trials (ocher), this time domain average does not reveal significant differences, as would be required to explain the observed MEG data as a consequence of eye position displacement.
Table S1 — related to Figure 2

<table>
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**Supplemental Experimental Procedures:**

**Participants:**

Twenty-two subjects (mean age 28 +/- 3.3, 10 females, 2 left handed) with normal or corrected-to-normal vision participated in the experiment. All participants provided their informed consent according to the local ethics committee and received monetary compensation for their participation.

**Stimuli and procedure:**

Stimuli were generated using Matlab (Mathworks Inc., Natick, MA) and the psychophysics toolbox [S1-S3]. At all times, a fixation point (white Gaussian with SD=0.3 deg of visual angle) was presented at the center of the screen. Following a fixation period of 1.25 seconds or more (see eye tracking procedure) one or two stimuli appeared on the screen. The stimuli were circular patches of stationary square wave gratings with a spatial frequency of 3.2 cycles/deg, a contrast of 100%, a diameter of 5 degrees of visual angle, positioned in the lower visual hemifields with their centers at 4 degree eccentricity, i.e. with the closest edge at 1.5 degrees from the fovea. Background was middle gray, and participants were monitoring the grating for a target event, i.e. the appearance of a small Gaussian contrast decrement within the grating. The magnitude of the contrast decrement was determined individually per subject, using a separate staircase procedure prior to the main experiment to achieve an average detection accuracy of 50%. Contrast decrements were limited to occur between eccentricities of 3.5 and 4.5 deg, i.e. within the overlap of a respective annulus and the grating. On half of the trials, displays contained two gratings on either side of fixation, and on the remaining trials unilateral gratings were presented. A single contrast decrement appeared in every trial, according to a flat probability distribution between 0.1 s and 3.44 s after stimulus onset. Button presses between 0.2 and 0.6 s after contrast decrements were considered correct responses (hits) and resulted in trial termination.

**Eye tracking procedure:**

Binocular eye position was recorded using an EyeLink 2K long-range eye tracker (SR research, Ontario, Canada) with the analog output recorded and stored with the MEG and EOG traces. Trials were not initiated until fixation was met for at least 0.5 s. Following 0.5 s of stable fixation, the trial was initiated, starting with the fixation period as described in the Stimuli and Procedure section. Participants were allowed to take advantage of this fixation criterion in order to take self-paced breaks within a block of trials by closing their eyes immediately after responding to a target (i.e., completing an experimental trial). Eye position was used to test whether any of the ongoing physiological dynamics predicting behavior resulted from a systematic displacement of eye position (see Results section).
Data acquisition and preprocessing:

Recordings were performed with a whole-head 275-channel axial-gradiometer MEG system (CTF Systems Inc., Canada). Horizontal and vertical EOGs were recorded simultaneously for off-line artifact rejection. All signals were low-pass filtered at 300 Hz, digitized at 1200 Hz and subsequently stored for off-line analysis.

All data analysis was done using Matlab (Mathworks Inc. Natick, MA) and the FieldTrip toolbox [S4]. Data were first preprocessed to remove trial parts with artifacts originating from jumps in the superconducting quantum interference devices (SQUIDS), muscle activity or eye movements using a semiautomatic routine. The 50 Hz line noise was removed using a discrete Fourier transform filter [S5]. Finally, trials were extracted from the data starting 1 s before stimulus onset until the target event occurred.

Source reconstruction:

In order to optimize signal-to-noise ratio and aid spatial interpretation, all analyses were performed at the source level. To estimate activity at the source level, we used adaptive spatial filters. The filters were based on the leadfield matrix of the individual subject (which in turn is based on the individual subject’s structural MRI) and the covariance, or cross-spectral density, matrix among the signals from all channels.

First, stimulus-induced gamma-peak frequency was determined per subject. For this, the sensor-level data were band-pass filtered in a broad gamma-band range (30-90 Hz), their time-domain covariance matrix was determined and used to generate spatial filters (linearly constrained minimum variance filters, LCMV). The filters were used to project the raw data into source space. For each source position, the spectrum of stimulus-induced power change was calculated by comparing the unilateral stimulus periods (0.3 s after stimulus onset until target event, cut into non-overlapping 0.5 s epochs) to the baseline period (last 1.25 s before stimulus onset, cut into non-overlapping 0.5 s epochs). The bilateral sources with maximal power changes were determined, and their average peak frequency was defined as the subject’s gamma frequency.

Second, for the subject’s gamma frequency, new spatial filters were calculated based on the cross-spectral density matrix, using dynamic imaging of coherence sources (DICS) [S6]. Those filters were based on the data from 0.3 s after stimulus onset until the target event, cut into non-overlapping 0.5 s epochs.

Finally, the DICS filters were used to estimate source-level gamma power time courses. For optimal temporal resolution, sensor-level data were spectrally analyzed with a sliding window, which had a length of 3 cycles of the subject’s gamma frequency and was moved in steps of 0.01 s. The resulting Fourier transforms were projected through the DICS-based spatial filters to arrive at gamma-power time courses for each source.

In order to combine source-level data over subjects, a regular 10 x 10 x 10 mm grid was defined in a standard brain [S7]. The brains of individual subjects were morphed into that standard brain, and the inverse transformation was applied to the regular grid in order to
determine the positions in each individual brain that corresponded to the regularly spaced grid sources in the standard brain.

**Phase consistency of the LGA fluctuation in hit versus miss trials:**

The main analysis used the source-level data excluding the first 0.3 s after stimulus onset in order to avoid onset-related response transients. The remaining gamma power time course was analyzed for windows centered between 0.54 s and 0.04 s before the target event, i.e. a 0.5 s window containing 50 samples of gamma power, end-aligned to shortly before the target event. These windows never contained data recorded after the target event, because all windows were less than ±0.04 s (0.08 s window length), because all subjects’ gamma frequencies were above 40 Hz and window length was defined as 3 gamma cycles long (i.e., maximally 0.075 s long).

The trials used to compare hit with miss trials always contained bilateral stimulation. All target events were unilateral, and each source grid point was coded as either contra- or ipsilateral to a given target event. The gamma-band power time courses of ipsilateral sources were subtracted from the homologous contralateral sources. This subtraction produced the lateralized gamma-band activity (LGA), which eliminates common gamma-power dynamics driven by the ongoing bilateral stimulation and captures inter-hemispheric gamma-power differences expected for attentional biases to one or the other stimulus.

The LGA was calculated for each trial and Fourier transformed to estimate, per frequency, the LGA phase relative to the target event. The trials were sorted into hit and miss trials, and for each possible pairing of hits and misses, the cosine of the phase difference was computed and then averaged over all possible pairs of hit and miss trials. This phase consistency metric (PCM) assumes a value of -1 if target events leading to hits versus misses are preceded by perfectly opposing LGA phases. It assumes a value of 1 if target events leading to hits versus misses are preceded by perfectly aligned LGA phases.

PCM was determined per source and frequency and subjected to group-level statistics. Statistical testing proceeded in two steps, using a t-test in a first step (which was not used to render the statistical inference) and a randomization test on spatial clusters of t-values including multiple comparison correction (which was used to render the statistical inference). T-tests (two-sided, one sample, separately per source location and frequency) were performed across subjects, comparing PCM against zero. Spatially adjacent sources with first-level p-values below 0.05 defined clusters, and the sum of t-values in a cluster was defined as the cluster-level test statistic. Observed cluster-level test statistics were compared against a randomization distribution, constructed as follows. For each of 1000 randomizations, 1) a random decision was taken per subject, to invert or retain the sign of the subject’s t-values (across all source locations and frequencies of that subject), 2) the cluster-level statistics was calculated as before, 3) the maximal cluster-level statistic across all sources and frequencies was placed into the randomization distribution. The observed cluster-level statistics were compared against the randomization distribution of cluster-level statistics. Observed values were considered significant if they were smaller than the 2.5th percentile or larger than the 97.5th percentile. The complete testing procedure implements
a non-parametric version of a two-sided random-effect test with multiple-comparison correction across all sources and frequencies [58].

We also source localized visually induced gamma-band activity. Per subject, all available non-overlapping epochs of 0.25 s of pre-stimulus baseline and of the stimulation period (excluding 0.3 s after stimulus onset) were used. Data epochs were multiplied with a single taper, giving a spectral smoothing of ±4 Hz, and Fourier transformed. FFTs of baseline and stimulation epochs were pooled for the generation of spatial filters with DICS. Subsequently, FFTs from all baseline and stimulation epochs were separately projected into source space. Source-level power for baseline and stimulation epochs were compared with an un-paired t-test. The resulting t-values were not used for statistical inference, but passed onto the group-level analysis. Group-level analysis proceeded as for the LGA source analysis above, except that multiple comparison correction was only required across space, because only the gamma band was source projected.

**Phase-by-accuracy analysis:**

We examined the modulation in performance as a function of 4 Hz phase of the LGA within the significant cluster found above, relative to the target event. Similar to previous work [59], we first determined the phase of optimal performance per subject and source. The average phase of miss trials was subtracted from the average phase of hit trials, revealing the phase of optimal performance. This optimal phase was used to realign all phases per subject and source, and subsequently bin them into eleven non-overlapping bins. Within each bin, per subject, an average accuracy was calculated. The optimal-phase bin, used for alignment, was excluded from further analysis to avoid circularity.

In order to establish the rhythmic profile of the phase-by-accuracy plots, a sine wave was fitted, per subject, with a fixed phase in order to determine the amplitude of performance modulation associated with the 4 Hz phase of the LGA. If the 4 Hz phase of the LGA indeed accounts for behavior, the hypothesis is that the amplitudes should be positive. To examine whether that was indeed the case, we performed a non-parametric randomization test. Specifically, in each of 1000 iterations contributing to the randomization distribution, the sign of the fitted sine wave was inverted for a random subset of subjects. Following the random sign inversion, a group average was calculated and added to the randomization distribution. The observed average was deemed significant if it was lower than the 2.5th or higher than the 97.5th percentile of the randomization distribution, corresponding to a non-parametric version of a two-tailed random-effect test.

**Cross frequency correlation analysis:**

To investigate potential cross-frequency coupling in the cluster shown in Figure 2, we used the same spatial filters to source project one-second epochs of raw data (one second non-overlapping epochs between stimulus onset plus 0.3 s and target event). Subsequently, we computed the FFT for lower frequencies as well as the gamma-band power time course and its FFT. Gamma-band power time courses per epoch were determined for three-gamma-
cycle windows (Hann-tapered) using individual subjects’ gamma frequencies, determined from the significant cluster identified in the main analysis (Figure 2). For the FFT of both gamma-power time courses and raw data, a Hann taper was used over each 1 s segment. Finally, pairwise phase consistency (PPC) was calculated for each trial between the lower frequency and the gamma-band power time courses [S10]. In order to establish statistical significance, a randomization distribution was created, by shuffling raw data and gamma-band power time courses from different epochs [S11].
Supplementary References


