

Current Biology

Distributed Attention Is Implemented through Theta-Rhythmic Gamma Modulation

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 16% of the average accuracy
- The 4 Hz modulation of gamma responses was evident throughout the attention period

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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-band 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 14.5% modulation in performance. These findings suggest that spatial attention is a theta-rhythmic sampling process that is continuously ongoing, with each sampling cycle being 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 and 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 electroencephalogram (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. For this idea to be incorporated 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 examination of 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, 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 quantification of attentional benefits as a function of time after 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 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 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

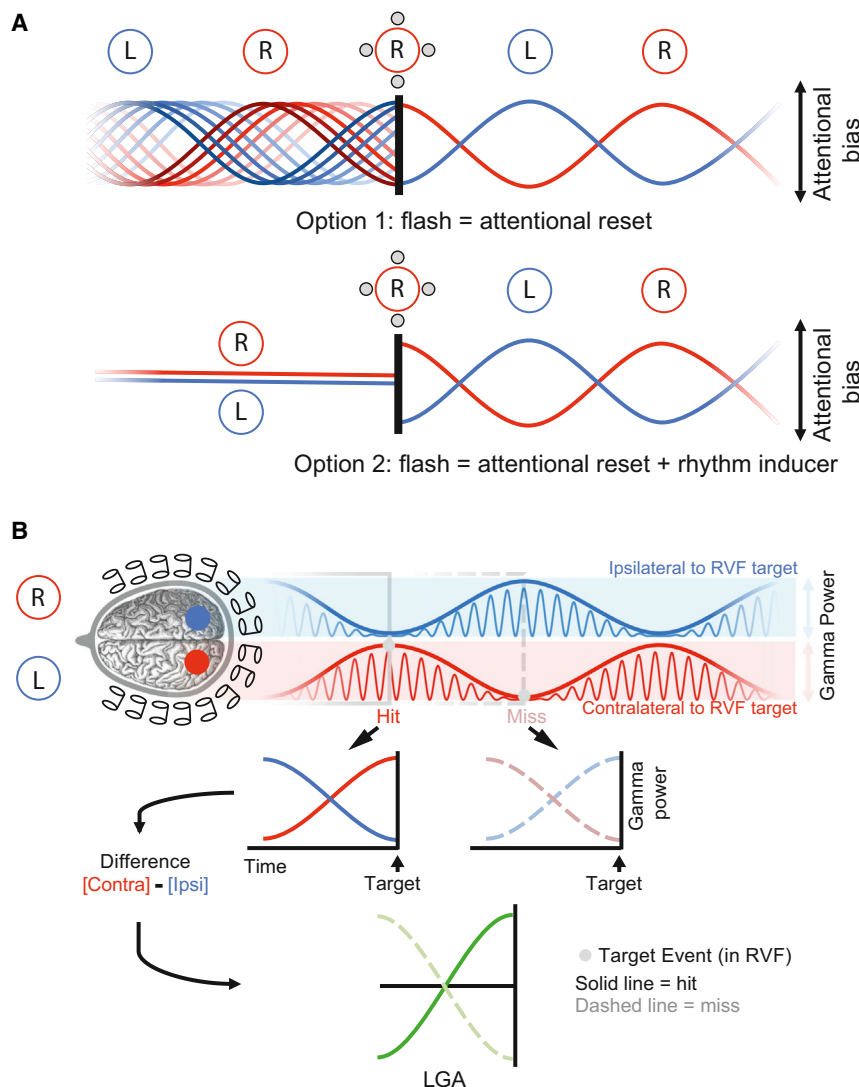


Figure 1. Schematic of the Attentional Sampling Hypothesis and Experimental Approaches Testing It

(A) Two alternative accounts of a previous psychophysical experiment, motivating the current magnetoencephalography (MEG) experiment, which is illustrated in (B). The psychophysical experiment utilized a reset event (four dots surrounding the circle presented at the time indicated by black vertical line) 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 (top; 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 (bottom; 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-band 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.

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 (either at sensor or 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

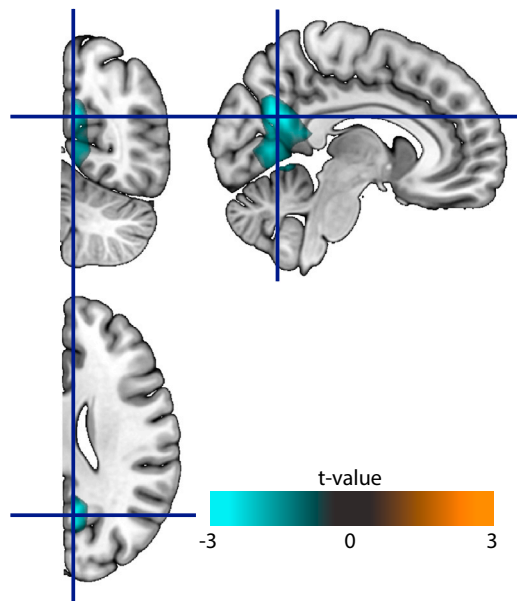


Figure 2. Sources with 4 Hz Anti-phase Relation between LGA Preceding Hits versus Misses

Significant negative cluster resulting from a group analysis of the 4 Hz LGA phase consistency metric for the hit versus miss trials (all combinations) over 22 participants. See also [Figure S1](#) and [Table S1](#).

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 PCM values are an indication of the 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 the [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 gyrus, and precuneus gyrus ([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

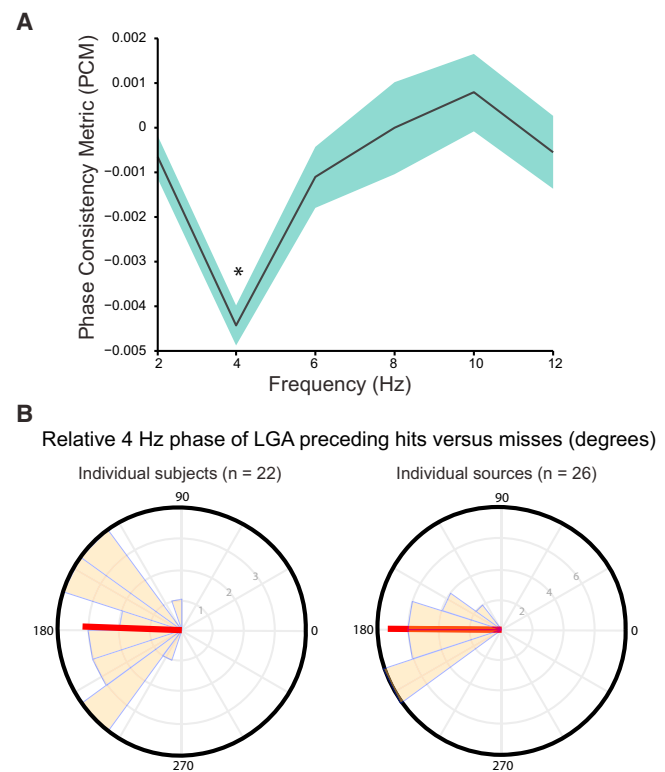


Figure 3. Further Characterization of the Source Cluster Shown in Figure 2

(A) 2–12 Hz LGA phase consistency metric for hit versus miss trials from the cluster displayed in [Figure 2](#). As can be seen, no other frequency demonstrates phase consistency except for the 4 Hz negative peak. The shaded region indicates the mean ± 1 SEM across subjects.

(B) Polar histograms of the mean phase difference of the 4 Hz LGA fluctuation between hit and miss trials for subjects (left; $n = 22$ subjects) and for sources (right; $n = 26$ sources).

See also [Figure S3](#).

timescale 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° , 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.

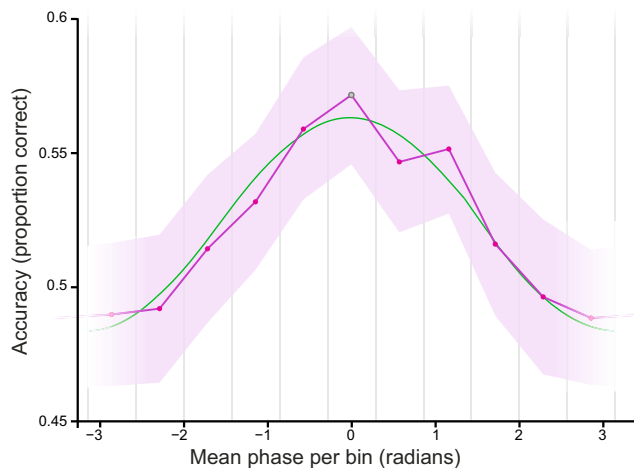


Figure 4. Detection Accuracy as a Function of the 4 Hz LGA Phase

Detection accuracy is plotted against binned 4 Hz LGA phase data from the significant cluster. The accuracy modulation depth (best to worst performance) is 14.5% of the average performance. Gray vertical lines denote the bin borders. Shaded purple region marks the SEM. The green line shows a sine wave fit.

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 ($t(21) = 10.6$, $p = 6.82 \times 10^{-10}$). At the level of individual subjects, the correlation was significant in 19 of 22 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^2 of 0.44. Consistent with that, performance differed significantly between

the peak-performance phase bin and the opposite phase bin ($t(21) = 7.27$, $p = 3.7 \times 10^{-7}$).

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. 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 the 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 the Supplemental Experimental Procedures), 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 that sustained attention distributed over two stimuli proceeds by continuously sampling them in alternation. In line with previous findings, we find biasing of the processing of one versus another attended object at 4 Hz, which is consistent with a sampling process at 8 Hz. Our findings suggest that the sampling process at theta is a spatially selective process, which entails better versus worse performance in one versus another behaviorally relevant location, rather than a general (i.e., spatially nonspecific) fluctuation in performance. Additionally, we further extend previous evidence for attentional

sampling that utilized a reset event to the case where no reset is present. This shows that the sampling mechanism is an ongoing process that does not require an external reset event.

Reset events of some sort have been contained in many previous attention studies. Tasks operationalizing exogenous attention always use a cue that draws attention to a particular stimulus. Tasks that implement endogenous attention often also include a cue onset [18]. Both variants of attentional tasks very often include a predictable temporal trial structure. Attention is of course at work also outside of attention tasks and is most likely indispensable for the interpretation of visual scenes [19]. Complex visual scenes require parsing into objects and the selective routing of those components to higher visual areas for interpretation [12]. The present results suggest that this selection occurs through the ongoing 8 Hz sampling process (but also see [20]). We speculate that the 8 Hz sampling process is fundamental to selection in general, such that temporally extended selection of a stimulus is implemented by repeated sampling that is preferentially directed toward that stimulus.

In a previous neurophysiological study, inferotemporal (IT) cortex neurons, which almost exclusively represent 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 most likely reset attention, we removed such reset events and based our 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 that LGA theta phase predicts 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](#).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.07.048>.

AUTHOR CONTRIBUTIONS

Conceptualization, A.N.L. and P.F.; Methodology, A.N.L. and P.F.; Investigation, A.N.L. and H.M.S.; Analysis, A.N.L., S.V.P., and P.F.; Writing, A.N.L. and P.F.

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