Phase of neural oscillations as a reference frame for attention-based routing in visual cortex

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A B S T R A C T

Selective attention allows the brain to efficiently process the image projected onto the retina, selectively focusing neural processing resources on behaviorally relevant visual information. While previous studies have documented the crucial role of the action potential rate of single neurons in relaying such information, little is known about how the activity of single neurons relative to their neighboring network contributes to the efficient representation of attended stimuli and transmission of this information to downstream areas. Here, we show in the dorsal visual pathway of monkeys (medial superior temporal area) that neurons fire spikes preferentially at a specific phase of the ongoing population beta (~20 Hz) oscillations of the surrounding local network. This preferred spiking phase shifts towards a later phase when monkeys selectively attend towards (rather than away from) the receptive field of the neuron. This shift of the locking phase is positively correlated with the speed at which animals report a visual change. Furthermore, our computational modeling suggests that neural networks can manipulate the preferred phase of coupling by imposing differential synaptic delays on postsynaptic potentials. This distinction between the locking phase of neurons activated by the spatially attended stimulus vs. that of neurons activated by the unattended stimulus, may enable the neural system to discriminate relevant from irrelevant sensory inputs and consequently filter out distracting stimuli information by aligning the spikes which convey relevant/irrelevant information to distinct phases linked to periods of better/worse perceptual sensitivity for higher cortices. This strategy may be used to reserve the narrow windows of highest perceptual efficacy to the processing of the most behaviorally relevant information, ensuring highly efficient responses to attended sensory events.

1. Introduction

Spike counts and patterns are used to represent sensory information in neural systems (Adrian and Zotterman, 1926; Arabzadeh et al., 2006; Heimendahl et al., 2007; Hopfield, 1995; Maunsell and Van Essen, 1983; Snowden et al., 1992). Independent of the magnitude of spike rate, the temporal structure of the individual spikes relative to the collective activity of neighboring population of neurons conveys information about the sensory stimuli. It has been shown that the phase of the oscillatory neuronal population activities where the spikes occur at, carries information in the neural systems of a wide range of animal models (Kayser et al., 2009; Montemurro et al., 2008). For example, Montemurro et al. previously reported that in the primary visual cortex (i.e., V1 of anaesthetized monkey), the phase of neuronal spikes (relative

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to low-frequency oscillations) provides additional information, exceeding the information that can be extracted from the spike rate alone (Montemurro et al., 2008). Recent research has provided evidence for the significance of the interaction between the spike times and the oscillatory phase in the ongoing population activity in association with high-level brain functions, such as visual attention (Chalk et al., 2010; Eghaie et al., 2018; Fries et al., 2001; Vinck et al., 2013; Voloh and Womelsdorf, 2018; Womelsdorf et al., 2014; Womelsdorf and Fries, 2007; Zareian et al., 2020), sensory processing (Eggermont and Smith, 1995; Fries et al., 2019; Safari et al., 2020), decision making (Pesar et al., 2008), and memory (Harris et al., 2002; Jacob et al., 2018; Kaminski et al., 2020; Lee et al., 2005; Siegel et al., 2009). In addition to information encoding (Kayser et al., 2012; Lisman, 2005; O’Keefe and Recce, 1993; Optican and Richmond, 1987; Siegel et al., 2009), this spike-phase coupling, as an indication of spike timing control, mediates the inter-neuronal synchronization of activity within a region, that is of particular importance for not only optimizing the inter-areal communication via the temporal coordination of postsynaptic potentials (Grion et al., 2016; Voloh et al., 2020; Womelsdorf et al., 2007; Zandvakili and Kohn, 2015), but also the performance of subjects’ perceptual decisions (Fiebelkorn and Kastner, 2021; Shahidi et al., 2019). There has been increasing evidence suggesting that the brain uses the phase of oscillatory population activities to distinguish information items via separate phase alignment of spikes. By shifting the phase relationship between the spike trains and the underlying oscillatory population activity in a systematic way, known as the phase shift phenomenon, the brain classifies spikes according to their information. Data from rodents indicate that spatial information is encoded at specific phases of the ongoing population oscillations for the hippocampal pyramidal cells (Dragoi and Buzsaki, 2006; Mehta et al., 2002; O’Keefe and Recce, 1993). Similarly, prefrontal neurons encode different memory contents at distinct phases, allowing the brain to store and separate different objects in memory concurrently (Siegel et al., 2009). This strategy may be exploited by the visual cortex to differentiate behavioral relevance of different information items.

Due to the brain’s limited resources to process the environmental information, selective information processing is crucial for an efficient processing of behaviorally relevant information, a cognitive function of the mammalian brain through which some aspects of environment gain advantage over nearby distractors, known as selective attention (Baluch and Itti, 2011; Desimone and Duncan, 1995; Maunsell and Treue, 2006; Petersen and Posner, 2012). Attention has been shown to affect visual neurons which represent the attended location/feature in a systematic way to enhance the neural representation and consequently the perception of behaviorally relevant (over irrelevant) sensory inputs which benefits behavior (Anton-Erxleben et al., 2007; Carrasco et al., 2004, 2002; Eghaie et al., 2022, 2015; Galashan et al., 2013; Katzner et al., 2009; Kozyrev et al., 2019; Roelfsema et al., 1998; Seidemann and Newsome, 1999; Treue and Martinez-Trujillo, 1999; Treue and Maunsell, 1996, 1999; Womelsdorf et al., 2006; Yao et al., 2016; Yeshurun and Carrasco, 2000, 1999; Yoo et al., 2022). More recently, several studies have suggested a temporal structure for spatial/feature-based attention (a rhythmic attentional sampling of the visual environment), reflected by the coupling of visual detection performance to the neural rhythms (Busch et al., 2009; Fiebelkorn et al., 2019, 2018, 2013; Helfrich et al., 2018; Landau et al., 2015; Landau and Fries, 2012; Li et al., 2016; Re et al., 2019; VanRullen, 2016). This rhythmic sampling is an indication of alternating periods of better and worse perceptual sensitivity (assigned to ‘good’ and ‘poor’ phase of collective neural activity, respectively) (Fiebelkorn et al., 2018; Landau and Fries, 2012; VanRullen et al., 2007).

Here we hypothesize that the phase of ongoing population oscillations (generated either internally or originating from feedback projections (Mejias et al., 2016; Michalareas et al., 2016; van Kerkoerle et al., 2014)) may provide an internal reference frame for discriminating sensory information of different behavioral relevance (see Jacob et al., 2018) for consistent observations for working memory). We conjecture that the preferred phase of spiking may be used as reference when encoding stimuli at the attended location to allow for a selective routing to downstream areas.

To test this hypothesis, we recorded from the medial superior temporal cortex (MST), an area in the extrastriate visual cortex of monkeys, with neurons selective to spiral motion patterns (Graziano et al., 1994; Wild and Treue, 2021). We simultaneously recorded local field potentials, as a proxy of the collective synaptic activity of local neuronal populations (Einevoll et al., 2013; Mazzoni et al., 2008; Mitzdorf, 1985), and single cell activity from two rhesus monkeys engaged in a visual attention task. We compared the neurons’ preferred spiking phase when they were encoding relevant vs. irrelevant sensory information. Our data and the results of our computational modeling support our hypothesis that the temporal pattern of single neuronal spikes is shaped by the phase of beta oscillations in the LFP, and importantly, spatial attention organizes spike times in order to discriminate relevant from irrelevant sensory inputs by aligning the spikes to different phases of beta oscillations. These results provide insight into how the information of attended stimuli, rather than unattended stimuli might be preferentially read out by downstream brain areas.

2. Results

Neurons fire spikes at specific phases of their neighboring network’s activity (O’Keefe and Recce, 1993). This spike-phase coupling represents the alignment of a neuron’s activity with the surrounding network. Here, we test the hypothesis that attentional allocation (to a specific spatial location or feature) modulates the alignment of the spikes’ timing to the phase of the local network’s oscillatory activity (Fig. 1).

To evaluate our hypothesis, we trained two rhesus monkeys to perform a visual attention task, where they covertly directed their attention towards one or the other of two spiral motion patterns. Monkeys N and W correctly performed the task in 91% and 89% of those trials where they maintained their eye fixation. We simultaneously recorded local field potentials (LFPs) and single unit activity from 90 direction-selective neurons in the visual cortical area MST. Depending on the spatial and non-spatial features (i.e., location and motion

![Fig. 1. Phase coding of selective attention. We hypothesize that the activity corresponding to different locations and features in the visual field dominantly occurs at distinct instantaneous phases of the local oscillations in the visual cortex’s population activity (phase coding). This implies that shifting the focus of attention from one stimulus to another shifts the timing of neuronal spikes between the two corresponding phase alignments. Therefore, changes in similarity between the focus of attention to the location and feature to which the sensory neuron is tuned, shifts the preferred spiking phase. Here, attention towards vs. away from the receptive field (RF) of a given neuron is depicted by different colors (orange and blue). Note that the preferred phase depicted here for the two conditions is arbitrarily selected.](image-url)
direction, respectively) of the attended stimulus relative to the recorded neuron’s preferred location (i.e., the receptive field (RF)) and feature (i.e., direction of motion), trials fell into two extreme attention conditions, maximally differing in their “feature-similarity” to the neuron’s preferences (feature-similarity gain model of attention (Martinez-Trujillo and Treue, 2004; Treue and Martinez-Trujillo, 1999)). In the attend-similar condition the feature-similarity was maximal, because the attended stimulus moved in the preferred direction inside the RF, while in the attend-nonsimilar condition the feature-similarity was minimal, because the attended stimulus moved in the anti-preferred direction outside the RF (Fig. 2A). Importantly, to maintain the sensory component of the neuron’s response at a high signal-to-noise ratio, the stimulus inside the RF moved towards the preferred direction in both attend-similar and attend-nonsimilar conditions.

As expected, the spike rate was significantly higher in the attend-similar than the attend-nonsimilar condition (Fig. 2B), replicating the well-known effect of combining spatial and feature-based attentional enhancement (Martinez-Trujillo and Treue, 2004).

Next, we estimated the phase of oscillatory activity in the LFPs to which spikes are preferably locked and compared it between attention conditions. Prior to computing the preferred spiking phase, we examined whether there is any meaningful rhythmicity in the recorded LFPs during the attention task. The mean power spectrum in Fig. 3A exhibits noticeable peaks in the delta-theta (~1 Hz) and beta range (~10–20 Hz). For a sample frequency range within beta (previously shown to underlie attentional processing in the dorsal pathway (Saalmann et al., 2007)), Fig. 3B and C show a phase-dependent rate of firing in MST during the trials.

Fig. 4A shows the frequency-resolved difference of the preferred LFP phase between trials when attention was directed into the neuron’s RF to the preferred-direction stimulus (attend-similar condition) or out of the RF to the anti-preferred-direction stimulus (attend-nonsimilar condition). We found that switching attention into the RF and to the preferred stimulus was associated with a significant positive phase shift of beta oscillations (19–24 Hz, paired Watson-Williams test, p < 0.05, false discovery rate [FDR] corrected). However, this shift of attention focus did not have a significant effect on the strength of spike-phase coupling within the beta frequencies (permutation test [n = 3000], p > 0.64 for all frequency bands, corrected for multiple comparisons - see Materials and Methods), suggesting that this frequency range is specifically involved in phase coding of neuronal spikes and not in modulating the synchrony between neurons (Esghaei et al., 2018; Kamechian et al., 2019).

Given that we did not observe a positive correlation between the spike rate and beta power (Pearson’s R = −0.16, p < 0.01) we can rule out a spurious coupling between spikes and LFPs within the beta range due to a leakage of action potential’s lower frequency components onto LFPs. Fig. 4A (right panel) plots the distribution of the preferred phases across neurons for the two attentional conditions for an example frequency range (18–22 Hz, highlighted in yellow in the left panel). These results indicate that the firing in the two attentional conditions aligns with different phases of the oscillatory activity of the surrounding network. This phase shift documents phase coding for attentional states, i.e., that different attentional states shift the spike alignment to different phases of the LFP. We therefore hypothesize that the phase shift is more pronounced for neurons that are more strongly modulated by attention.

To test this, we next removed those neurons with a weak attentional index (AI < 0.1, see Materials and Methods). The right panel of Fig. 4B presents the neuron-wise phase shift distribution averaged across the frequency bands with a significant positive modulation (15–26 Hz). In line with our hypothesis, the attentional phase shift for these neurons is more pronounced (0.80 and 0.08 rad for AI > 0.1 and AI < 0.1, respectively; Watson-Williams test over the average phase shift across

Fig. 2. Behavioral task to study selective attention. (A) Schematic depiction of the trial evolution for two attentional conditions. After the monkey fixed its gaze on the central fixation point and pressed a lever, an eccentric spatial cue (static random dot pattern (RDP)) was presented to guide the animal’s spatial focus of attention. After a blank period, two incoherently moving RDP masks were displayed at an equal eccentricity (one inside and the other outside the RF (gray-filled circle)), followed by two spiral motion patterns moving in the preferred direction (illustrated by expansion motion-P) or the anti-preferred direction (contraction motion-N). The monkeys were rewarded when they responded to a transient speed increment (occurring at a random instant between 250–2500 ms after stimulus onset) in the target stimulus (indicated by a dashed circle), while ignoring the speed change in the distractor. Attentional conditions are shown by the colors orange (attend-similar) and blue (attend-nonsimilar). (B) Normalized spike density functions across MST neurons (calculated with Gaussian kernel with σ = 15 ms). Time 0 indicates the onset of spiral motion patterns and the vertical dotted lines indicate the analysis time range. Error bands represent the standard error of the mean (SEM).
frequency bands with a significant shift—panel A, p = 0.017). One could argue, that the phase alignment of spikes to the LFP reference is changed by differences in response latencies, caused by stimulus or behavioral differences (Bair et al., 2002). Such an effect would be expected to quickly peter out in the course of trial. However, an attentional phase shift is present even in late parts of our trials (Fig. S2).

We did not include the lone significant negative phase shift (centered at 9 Hz) into this plot, because it is only significant for the subset of data plotted in Fig. 4B and not for Fig. 4A. In addition, this data point (other than the significant positive phase shifts) is neighbored by non-significant data points that also have inhomogeneous phase shifts across neurons (indicated by the white background).

We next asked if the attentional phase shift changes as a function of attention level. It has been well-established that behavioral reaction time is negatively correlated with attention level (Carrasco, 2011; Parto Dezfooli et al., 2018; Posner, 1980; Womelsdorf et al., 2006). Therefore, we focused on the link between the magnitude of the phase shift and the behavioral response. To this end, we determined the relationship between the attentional phase shift and the monkeys’ reaction time (RT) for detecting the target change. The trials were first sorted into four quartiles based on their RT and the phase shift was calculated for the first and fourth quartile (short RT and long RT, respectively). Fig. 5 shows that the attentional phase shift in the beta range is only significant for short RT trials. Furthermore, while the association of phase to behavior is observed in both attend-similar and attend-nonsimilar trials (Fig. S4), the observation of a phase shift between attend-similar and attend-nonsimilar is not associated to RT differences between the two attentional conditions (Fig. S5). Our observed attentional phase shift is also not an artifact of a potential difference in the response event (stimulus speed change) time between short RT and long RT trials (Fig. S6). This fits our observation that the attentional phase shift is strong and significant only for fast responses (when attention level is high). For a similar analysis of incorrect trials see Fig. S7.

Given that attend-similar and attend-nonsimilar trials differ in both the attended location and attended direction of motion, we next examined if the observed shift in MST neurons’ preferred spiking phase is selectively caused by the switch in the focus of spatial or of feature-based attention. To this end, we added a new type of trial, where the animal’s spatial attention was directed to the stimulus outside the RF, which was moving in the preferred-direction (combining a non-spatial feature (i.e., direction) similar to the neurons’ selectivity with a nonsimilar spatial feature (i.e., location)). By comparing the neural responses evoked in these trials, with those of the attend-similar and attend-nonsimilar conditions, we isolated the effect of spatial and feature-based attention, respectively. Our data show that a phase shift occurs only when spatial attention is shifted between the inside and outside of a RF, not when feature-based attention is switched between the anti-preferred and preferred direction (Fig. 6; spatial attention: paired Watson-Williams test, p < 0.05, FDR corrected; feature-based attention: paired Watson-Williams test, p > 0.52, FDR corrected).

As a straightforward hypothesis, the underlying mechanism of the attentional phase shift may involve a time shift (delay) in generating the spikes in post-synaptic neurons (see Basalyga et al., 2013; Burgess and O’Keefe, 2011; Mysin et al., 2019; Yamaguchi et al., 2008) for alternative approaches). The location of such a transmission delay could be the synaptic input to MST neurons (Barardi et al., 2014; Palmigiano et al., 2017). To test this, we built a simple computational model. The model is constructed of two connected neural populations, representative of the sensory and regulatory subnetworks, each consisting of excitatory and inhibitory neurons. All of the model neurons can receive excitatory/inhibitory postsynaptic potentials from neurons of the same or the other subnetwork. Furthermore, external drives to the model neurons are adjusted so that the two subnetworks show oscillatory activity predominantly at frequencies around 40 and 20 Hz (for the sensory and regulatory network, respectively - see Materials and Methods). We next applied different levels of delay to the postsynaptic potentials to influence the coupling of sensory neurons to the modulatory subnetwork’s beta rhythm. We observed that, by increasing the synaptic delay, sensory neurons start to shift their preferred spiking phase relative to the modulatory beta oscillations (Fig. 7), presumably due to a delayed effect of the modulatory subnetwork on the sensory neurons. These results suggest that the neural mechanism underlying the attentional shifts of the phase-alignment of neuronal firing, may involve controlling the synaptic delay of inter-neuronal connections within a sensory area (Fig. S8). However, our modeling results do not address the potential relationship between specific synaptic delays and alignment to a specific phase of LFP. Future studies should investigate whether introducing the delay will only shift the responses in time or could also maintain an alignment to a specific phase of the LFP. As we do not observe a consistent phase shift within the theta band in MST, it also remains an open question how synaptic delay corresponds to phase shifts within a specific frequency band.

In summary, our data suggest that the spatial focus of attention (but not the focus of feature-based attention) is coded in the spike timing of MST neurons relative to the phase of the local neural network’s oscillatory activity. We further found that this phase difference’s magnitude

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**Fig. 3.** Power spectrum of LFPs and the coupling of spikes to LFP phase. (A) The black line represents the mean power spectrum in MST. Power spectrums of recorded LFPs in different sessions are shown in gray. (B) The phase-resolved firing rate distribution for each neuron. Neurons are sorted based on the phase with the smallest spike density (Y-axis). For a sample frequency band with a local peak in power (21–25 Hz), we computed the rate of spikes within different phase bins (bin-size = 2π/15) and normalized it between 0–1 for each trial. For each condition we averaged the phase-based distributions across the corresponding trials and next, computed the mean distribution across the two conditions for each neuron. (C) The distribution of the preferred spiking phase indicating that MST neurons tend to fire around the trough of beta oscillations (Rayleigh test for circular uniformity, p < 0.01). For each neuron we calculated the preferred spiking phase relative to the beta oscillations by averaging the neurons’ locking phase across the two attentional conditions (see Materials and Methods). The visualized smoothed color plot is based on a phase resolution of 19 non-overlapping bins.
depends on the attentional performance (reflected in the reaction times) of the subjects and exclusively occurs at higher attentional levels.

3. Discussion

Here, we investigated whether the temporal alignment of the discharges of single neurons relative to the phase of oscillatory activities in their neighboring neuronal network (captured by the LFP) plays a functional role in relaying the attended stimulus’ information. Our data reveal that: first, neuronal spikes are locked to a specific phase of beta oscillations of the LFP in the macaque visual cortical area MST. Second, spatial attention modulates this preferred phase of the locking and that this modulation is especially pronounced for neurons strongly modulated by attention. Third, the attentional shift of the preferred beta phase is predictive of the subsequent behavioral response time of animals. Our computational model shows that this attentional shift of the preferred phase may be associated to a so-called attentional lag of post-synaptic potentials within the network of sensory areas.

In our study we observed that spikes preferentially cluster at different phases of the ongoing beta rhythm of LFP oscillations depending on the spatial focus of attention (Fig. 1). This observation suggests that attended/unattended sensory information are channeled by different phase ranges of beta oscillations. Specifically, we observed that with the shift of spatial attention from the outside to the inside of the RFs, spikes tend to occur at a later phase of the beta oscillations (Fig. 4A); a shift that is only significant when attention levels are high (i.e., at short RTs). This feature of the MST network may allow downstream areas to decode the locus of attention from sensory neurons using the timing (in addition to the rate) of spikes relative to the neighboring population. The neural mechanism for reading out the focus of attention in downstream areas is a question for future studies.

While the role of gamma oscillations as a gating mechanism for visual attention is well-recognized, an involvement of beta oscillations in attentional processes is gradually becoming apparent. Historically
linked to motor control and top-down processing, beta oscillations have more recently been linked to sensory perception and attention (Engel and Fries, 2010; Lee et al., 2013). Importantly, beta oscillations stemming from the fronto-parietal attention-control network have been observed to adaptively modulate the bottom-up signals of sensory neurons (Bastos et al., 2015; Shaverdi et al., 2023). This modulation is designed to enhance behavior depending on the spatial attention’s focus, signifying a sophisticated interplay between top-down and bottom-up processes. Previous studies have also underscored the role of beta rhythms in determining the efficacy of feed-forward projections in sensory regions, including MST (Buschman and Miller, 2007; Donner et al., 2007; Michalareas et al., 2016; Richter et al., 2017). Furthermore, it is pertinent to mention that beta oscillations can modulate feed-forward signals through phase-amplitude coupling with gamma rhythms, suggesting a nuanced interaction between these oscillatory frequencies. Within the realm of visual attention, beta oscillations might be crucial in reinforcing the neural representation of the attended sensory input against potential distractors. Thus, while our observed phase alignment effect in the beta range might initially appear surprising, it offers insights into the intricate oscillatory dynamics that scaffold attentional processes, emphasizing the multifunctionality of oscillatory frequencies in mediating attention.

Our data further indicate that the attentional phase shift is linked to the attention level (indicated by behavioral reaction times), i.e., attentional phase shifts are only present when reaction times are short. A large attentional phase shift can be interpreted as a sharper distinction of the attended and unattended information, helping to encode the attended information more efficiently by assigning the limited processing epochs to the most relevant stimuli in the scene. A sufficiently large attentional phase shift allows the attended stimulus to be selectively transmitted to higher cortical areas and read out with minimal distortion by the surrounding noise (the unattended stimuli).

Unlike the classic view suggesting that spatial attention samples the visual space continuously, several recent studies have observed a rhythmic sampling by spatial attention (Fiebelkorn et al., 2019, 2018; Fiebelkorn and Kastner, 2019; Helfrich et al., 2018; Landau and Fries, 2012; VanRullen et al., 2007). Consistently, our results also indicate that MST neurons transmit the information of the attended stimulus to higher cortices through oscillatory beta-aligned periods of enhanced coding for the attended stimulus. Future studies need to examine the existence of a beta-aligned perceptual sensitivity for motion recognition.

One could interpret a stimulus’ location in visual space as a feature in the visual feature space. Similarly, a neuron’s receptive field could be interpreted as the neuron’s preferred feature in location-space. Therefore, both types of attention modulate neurons’ responses based on the similarity of the attended feature relative to the neuron’s preferred feature (Maunsell and Treue, 2006; Treue and Martínez-Trujillo, 1999).

**Fig. 5.** Reaction time (RT) varies as a function of phase shift. The observed phase shift within the beta range is mainly observed for trials with a short RT (fast behavioral responses). Inset: distribution of RTs in each attentional condition. The first (red) and fourth (yellow) quartiles are referred to as short and long RT, respectively.

**Fig. 6.** Attentional phase shift is dominated by spatial, rather than feature-based attention. The blue-green curve (for feature-based attention) shows the phase difference between attend-out-pref and attend-nonsimilar (attend-out-antipref), whereas the orange-green curve (for spatial attention) presents the phase difference between attend-similar (attend-in-pref) and attend-out-pref conditions. The horizontal lines indicate the frequencies with a significant attentional phase shift for the corresponding attention type.

**Fig. 7.** Synaptic delay of postsynaptic potentials adjusts the timing of spikes relative to the phase of the modulatory network. Our computational model reveals that the predominant phase of spiking activity of sensory neurons relative to the population’s beta oscillations is correlated with synaptic delay. The X-axis represents the synaptic delay applied to the timing of postsynaptic potentials and the Y-axis represents the phase of coupling relative to that when there is no synaptic delay.
Therefore, one might wonder whether the neural activity influence exerted by spatial and feature-based attention may have identical encoding mechanisms. However, this is in contrast to our finding regarding the modulation of firing phase, which demonstrates the neuronal modulation of locking phase is exclusively caused by spatial attention. Spatial attention takes advantage of firing phase through an exclusive mechanism to enable the visual system to selectively process the attended stimulus in a more efficient manner. This supports the hypothesis that spatial and feature-based attention do not use the same mechanisms. Spatial attention modulates both firing rate and the preferred firing phase of neurons, whereas feature-based attention is not observed to modify the preferred firing phase.

One question is whether attentional phase coding follows a topographic map or not, i.e., if the distance between an attended and unattended stimulus (proportional to the distance between the RFs of the neurons representing them) is correlated with the magnitude of the attentional phase shift. This is particularly important when asking if the beta phase can serve as an internal reference frame for distinguishing the attended stimulus from other stimuli. This exceeds the scope of the present study and thus remains a question for future studies.

Our findings, the pronounced phase tuning associated with spatial features, contrasted with the absence of such tuning in feature-based attention shifts, demonstrate the need for a better understanding of the neural computations that govern attentional processes. To optimize performance in our behavioral task, it is conceivable that the neural decoder of the stimulus representation relies on the simultaneous and integrated processing of inputs from both preferred and anti-preferred neurons with overlapping spatial preferences. This intricate balance ensures that information—both from neurons with tuning preferences and those opposed to them—is uniformly and effectively transmitted to the subsequent neural processing levels. Such concurrent processing offers an efficient strategy. By not allowing neurons with anti-preferred features to be selectively inhibited by the LFP phase, the system potentially preserves a richer dataset of visual information, thereby increasing the likelihood of a successful behavioral response.

Together, our data show that action potentials in area MST of macaque visual cortical are locked to the phase of beta oscillations in the LFP and spatial attention significantly shifts this locking phase. We suggest that attention changes the locking phase to transmit relevant visual information during an exclusive period within the oscillatory cycle optimized for a higher perceptual sensitivity in higher cortices.

4. Materials and methods

Research with non-human primates represents a small but indispensable component of neuroscience research. The scientists in this study are aware and are committed to the great responsibility they have in ensuring the best possible science with the least possible harm to the animals (Roelfsema and Treue, 2014; Treue and Lemon, 2023).

Methodological details concerning our animal subjects, their holding and welfare, our experimental permits, surgeries and implants as well as details of the experiments were reported previously (Esghaei and Daliri, 2014; Khamechian et al., 2019; Ray et al., 2021; Xue et al., 2017; Yao et al., 2018; Zareian et al., 2020). We reiterate relevant details here.

4.1. Subjects and animal welfare

Data were collected from two rhesus monkeys (Macaca mulatta, Monkey N, Monkey W, both 12-year-old males). Area MST was accessible through a recording chamber implanted over the parietal lobe based on a magnetic resonance imaging (MRI) scan (right hemisphere for Monkey W, left hemisphere for Monkey N). Each monkey was implanted with a titanium head holder to minimize head movements during the experiment. Both monkeys were seated in custom-made primate chairs and head-fixed during the experiment.

All animal procedures of this study were approved by the responsible regional government office (Niedersaechsisches Landesamt fuer Verbraucherschutz und Lebensmittelsicherheit (LAVES)) under the permit number 33.14.42502-04-064/07 and were performed in full accordance with relevant guidelines and regulations.

The animals were pair- or group-housed in the facilities of the German Primate Center (DPZ) in Goettingen, Germany. The facility provides the animals with an enriched environment (including a multitude of toys and wooden structures (Berger et al., 2018; Calapai et al., 2023, 2017)), natural as well as artificial light, exceeding the size requirements of the European regulations, including access to outdoor space. The animals’ psychological and veterinary welfare was monitored by the DPZ’s staff veterinarians, the animal facility staff and the lab’s scientists, all specialized in working with non-human primates. During the study the animals had unrestricted access to food and fluid, except on the days where data were collected or the animals were trained on the behavioral paradigm. On these days, the animals were allowed access to fluid through their performance in the behavioral paradigm. Here the animals received fluid rewards for every correctly performed trial.

Surgeries were performed aseptically under gas anesthesia using standard techniques, including appropriate peri-surgical analgesia and monitoring to minimize potential suffering. The two animals were healthy at the conclusion of our study and were subsequently used in other studies.

We have established a comprehensive set of measures to ensure that the severity of our experimental procedures falls into the category of mild to moderate, according to the severity categorization of Annex VIII of the European Union’s directive 2010/63/EU on the protection of animals used for scientific purposes (see also (Pfefferle et al., 2018)).

4.2. Electrophysiological recordings and behavioral task

Experiments were performed in a dim room and the procedure for stimulus presentation, monitoring the eye position and recording neural and behavioral data during the experiment were controlled using a custom computer program running on an Apple Macintosh PowerPC. We monitored the eye position using a video-based eye tracker (ET49, Thomas Recording, Giessen, Germany). Visual stimuli appeared on a computer monitor at a refresh rate of 75 Hz and a spatial resolution of 40 pixels per degree. The monitor was placed at a distance of 57 cm from the animals covering approximately $40' \times 30'$ of visual angle.

During 86 sessions (monkey N: 37 sessions; monkey W: 49 sessions), we recorded the local field potentials and action potentials of 40 single units from monkey N and 50 single units from monkey W while performing a visual attention task. Given the tailoring of the stimuli to the preferences of a single neuron, we typically only recorded one neuron at a time. Given the demanding behavioral task and the need for a substantial number of correctly completed trials we usually recorded not more than one neuron during a recording session. The extracellular neuronal activity was recorded using a three-channel microdrive system (Mini Matrix; Thomas Recording) and a multichannel acquisition processor system (Plexon Inc., Dallas, TX), running at a sampling rate of 40 kHz. Action potentials were sorted online (waveform window discrimination, Sort Client; Plexon Inc.). Area MST was localized by referencing the recordings to the structural MRI and identified by the physiological properties of the recorded neurons (large RFs compared to neurons of the mediotemporal area MT, as well as direction tuning to spiral motion (Graziano et al., 1994)). After isolating a neuron, its RF was estimated by manually moving a static stimulus on the monitor while the monkey maintained its eye gaze on the fixation point to report a luminance decrease and receiving a reward. The dataset analyzed here also served as the basis for another publication (Xue et al., 2017) with a focus on firing rate patterns.

Compared to lower-level areas in the motion processing pathway (such as area MT), MST neurons show a unique selectivity and responsiveness to spiral motion patterns. Correspondingly we presented a series of spiral motion patterns in the RF in order to determine the preferred...
stimulus of the neuron (Wild and Treue, 2021). Each of these patterns consisted of small bright dots (with a dot density of 8 per square degree and luminance of 75 cd/m^2) moving within a stationary circular aperture (4° of visual angle) on a gray background with a luminance of 35 cd/m^2. Spiral motion stimuli form a ‘spiral motion space’ where expansion, clockwise rotation, contraction and counterclockwise rotation are neighboring stimuli, with a continuum of stimuli in between these cardinal directions (Graziano et al., 1994; Ilos and Freedman, 2016; Wild and Treue, 2021). The direction of a specific spiral motion stimulus is determined by the angle that the direction of all of its individual dots form with radial reference lines. By varying this angle by equal steps, we created 12 different spiral stimuli, evenly covering the spiral motion space. The direction eliciting the highest neuronal response was taken as the preferred direction of the unit, while the opposite direction was labeled as the anti-preferred direction (equivalent to the approach taken for linear motion tuning in lower-level areas in the motion processing pathway).

We trained two monkeys to perform a visual attention task (Fig. 2A), in which they had to locate a central fixation point (0.2° × 0.2° of visual angle) and initiate each trial by pressing and holding a response lever. After 146 ms, a stationary random dot pattern (RDP) appeared as a spatial cue for 67 ms at the location where the animal had to attend covertly. Afterwards, the cue disappeared, and following 400 ms of blank period, two incoherently moving RDPs were presented on the right and the left side of the screen. One of these RDPs was placed in the recorded neuron’s RF, while the other one was placed outside the RF at an equal eccentricity from the fixation point. After 375 ms, the RDP in the neuron’s RF was replaced by the preferred spiral motion pattern and the RDP located outside the RF at the opposite hemi-field was replaced by either a preferred or anti-preferred spiral motion pattern. The incoherently moving RDPs served to mask any potentially remaining afterimage of the cue. The 775 ms long interval (comprised of blank and mask periods) between the cue offset and the target onset additionally ensures that any differences in responses to the target and distractor are not caused by the preceding absence or presence of the cue stimulus. Importantly, the stimulus inside the RF always moved towards the preferred pattern of the neuron. The stimulus at the cued and non-cued location is referred to as ‘target’ and ‘distractor’, respectively. To receive a liquid reward, the animals had to release the lever in response to a transient speed increment (occurring at a random instant between 250–2500 ms after the onset of spiral motion patterns) in the target while ignoring any speed changes in the distractor. Depending on whether the cued stimulus matched the recorded neuron’s spatial and non-spatial properties (i.e., neuron’s RF and preferred motion direction), trials were divided into two distinct groups; 1) Attend-similar, where the target stimulus was placed inside the recorded neuron’s RF and moving towards the preferred direction (cued stimulus matched both spatial and non-spatial properties of the recorded neuron), and 2) Attend-nonsimilar, where the target stimulus was placed outside the recorded neuron’s RF in the opposite hemi-field and moving towards the anti-preferred direction (neither of the spatial and non-spatial properties of the recorded neuron matched the target). By comparing the neuronal responses between these two attentional conditions we investigated the extreme cases of selective attention. Furthermore, we interleaved these trials with a third type of trials (attend-out-pref) in which attention was directed away from the recorded neuron’s RF within which a stimulus was moving towards the preferred direction (cued stimulus matched solely the non-spatial property of the recorded neuron). Through comparing the neuronal responses evoked in this condition with those evoked in the Attend-similar and Attend-nonsimilar condition, we isolated the effect of spatial and feature-based attention, respectively.

4.3. Data analysis

For all analyses, we used all correctly performed (hit) trials from the two animals and the data were analyzed using customized scripts in MATLAB, as well as the EEGLAB and CircStat toolboxes.

For all statistical tests, alpha level for the decision criterion was chosen to be 0.05 and to overcome the problems due to multiple testing, we used the false discovery rate (FDR) approach to determine adjusted p-values (based on the number of performed tests).

4.4. Spike rate quantification and analysis window

To estimate changes in spike rate over time, the spike density function (SDF) was computed by convolving the spike train from each trial with a Gaussian kernel of SD = 15 ms. For each unit, SDFs were averaged across trials of the same attentional condition and normalized to the maximum value across the two conditions’ average SDFs. The SDFs began to diverge between the two attentional conditions 67 ms after the stimulus onset (permutation test (n = 3000), FDR adjusted p-value < 0.05) (Fig. S9).

To ensure that all of the analyses focus on the sustained (rather than the transient) component of the spiking activity and the LFP, our analysis window (duration: 500 ms) starts 350 ms after the onset of the spiral motion patterns. To avoid any contamination of the neural responses by stimulus or behavioral changes, we included only trials where the speed change occurred after the analysis window.

4.5. Attentional index measurement

To assess attention’s effect on spike rate, we calculated the attentional index (AI) for each recorded neuron within the interval of 350–850 ms after stimulus onset by comparing neuronal responses in the two different attentional conditions using the following formula:

\[
AI = \frac{(SR_{\text{Attend-similar}} - SR_{\text{Attend-nonsimilar}})}{(SR_{\text{Attend-similar}} + SR_{\text{Attend-nonsimilar}})}
\]

where SR_{Attend-similar} and SR_{Attend-nonsimilar} are the mean spike rate when attention was directed towards the preferred stimulus in the RF or towards the anti-preferred stimulus outside the RF, respectively.

4.6. Spike-LFP phase coupling

For each recorded spike-LFP pair, we first band-pass filtered the LFP signals in 35 overlapping frequency bands with the bandwidth of 4 Hz and starting frequencies from 2 to 36 Hz (using eegfilt function from EEGLAB toolbox with an order of 3 “sampling rate/low cutoff freq”) and then measured the similarity of phases where the spikes coincided with, at different frequency bands by defining the complex number \( z \) that is equivalent to the ‘power-biased circular sample mean’ of the phase distribution of spikes which occurred during the associated trial. In a single trial, the \( z \) vector (at different frequency bands of LFP) was calculated using the following equation:

\[ z = \frac{1}{n} \sum_{k=1}^{n} \phi e^{j\psi} = re^{j\psi} \]

where \( \phi \) and \( \psi \) represent the instantaneous phase and power of the filtered LFP, respectively determined by the argument and absolute value of Hilbert transform at the instant that the kth spike occurred and \( n \) is the total number of spikes occurring during each trial. The factor \( r \) weights the spike phases proportional to the instantaneous power, allowing spike phases measured with a higher signal to noise to proportionally have a large effect on the resultant vector. The complex number \( z \) can also be rewritten with parameters \( r \) and \( \psi \) (known as Kuramoto order parameters) which capture the strength of coupling and the locking phase, respectively. At a constant power, \( \psi \) is higher when spikes tend towards an identical phase and lower when spikes are uniformly distributed across the phase space. At each frequency band we obtained two \( \hat{z} \) vectors (corresponding to the two attention conditions) for each neuron by calculating the circular average of the \( z \) vectors across trials (weighted by the average power of the filtered LFP within each trial) of
each attention condition. To do so, we utilized the following equation:

$$Z = \frac{1}{N} \sum_{i=1}^{N} \alpha_{i} e^{\nu_{i}}$$

where \(\nu_{i}\) and \(\alpha_{i}\) are the \(x\) vector’s phase and the filtered LFP’s average power (respectively) corresponding to the \(i\)th trial, and \(N\) is the neuron’s number of trials in each attend-similar/attend-nonsimilar condition.

By subtracting the phases of \(Z\) vectors between attention conditions (attend-similar – attend-nonsimilar) we determined the attentional phase shift and then by taking the absolute values of \(Z\) vectors we estimated the strength of spike-phase coupling assigned to the two attention conditions for each neuron. Therefore, we had 35 phase shift distributions for 35 frequency bands and by calculating the circular mean of each of them we determined a mean attentional phase shift within each frequency band (Fig. 4). We examined for the similarity of the phase shift across neurons, by applying a Rayleigh test for non-uniformity of the phase shift distributions in each frequency band (gray filled areas in Fig. 4 indicate frequency bands in which the phase shift data is sampled from a von Mises distribution). Afterwards we examined each of the frequency bands to see if there was a phase shift distribution with a mean unequal to zero by applying a paired Watson-Williams test (as a one-way ANOVA test for circular data).

### 4.7. RT quartile boundaries

For selecting the first and fourth quartiles, we selected the RT thresholds such that the number of trials falling within each quartile was equal or higher than 25% of the total number of trials for each attention condition. The following table shows the details after choosing 296 and 354 ms as thresholds for first and fourth quartiles, respectively.

| Condition               | # of selected trials for first quartile | # of selected trials for fourth quartile |
|-------------------------|----------------------------------------|----------------------------------------|
| Attend-similar          | 173 out of 592                         | 158 out of 592                         |
| Attend-nonsimilar       | 171 out of 651                         | 196 out of 651                         |

### 4.8. Modeling

Implementing a previously proposed neural network architecture for area MT/MST (Esghaei et al., 2018), we combined a sensory and a regulatory subnetwork. The sensory subnetwork predominantly represent sensory information (here, motion direction), while the regulatory subnetwork coordinates the neural dynamics of the sensory subnetwork (for more information on this architecture, see Esghaei et al., 2018; Kopell et al., 2010; Tort et al., 2007). Our computational model of each subnetwork is based on two influential models which optimally represent network-level neural interactions reflected by LFPs (Börgers et al., 2005; Palmigiano et al., 2017). Each subnetwork is composed of 200 model neurons: 80% excitatory (\(N_{E}\)) and 20% inhibitory (\(N_{I}\)). The excitatory and inhibitory model neurons use the Hodgkin-Huxley model (Hodgkin and Huxley, 1952) as a well-established and biologically plausible computational model of a neuron’s dynamics of the membrane potential (Barardi et al., 2014; Palmigiano et al., 2017). The probability of establishing excitatory and inhibitory projections (\(P_{E}\) and \(P_{I}\), within/between subnetworks) are 0.3 and 0.2, respectively (as proposed and examined by Palmigiano et al., 2017).

This model defines the membrane potential \(V\) and ionic gating variables as the following:

$$C_{m} \frac{dV}{dt} = g_{Na} m^{3} h \left(V_{Na} - V\right) + g_{K} n^{4} \left(V_{K} - V\right) + g_{L} \left(V_{L} - V\right) + I_{app} + I_{in}$$

$$\frac{dx}{dt} = a_{x}(V)(1 - x) - b_{x}(V)x \quad (x = n, h, m)$$

where \(C\), \(V\), \(t\) and \(g\) denote capacitance density (\(\mu F/\text{cm}^{2}\)), voltage (mV), time (ms), ionic conductance density (\(ms/\text{cm}^{2}\)) and current density (\(\mu A/\text{cm}^{2}\)), respectively. \(a\) and \(b\) are functions of the membrane potential (measured in \(mV^{-1}\)) and for gating variable \(m\) we used the following assumption: \(m = m_{in}(V) = \alpha_{m}(V)/[\alpha_{m}(V) + \beta_{m}(V)]\).

The constants and time rate functions of our excitatory neurons are (Börgers et al., 2008):

$$C = 1, g_{Na} = 100, V_{Na} = 50, g_{K} = 80, V_{K} = -100, g_{L} = 0.1, \text{ and } V_{L} = -67, \text{ and } \alpha_{m}(V) = 0.32(54 + V)/[1 - \exp(-0.25(V + 54))], \beta_{m}(V) = 0.28(27 + V)/[\exp(0.2(V + 27)) - 1], \alpha_{n}(V) = 0.128\exp(-(V + 50)/18), \beta_{n}(V) = 4/[1 + \exp(-(V + 52)/18)], \alpha_{h}(V) = 0.032(52 + V)/[1 - \exp(0.2(V + 52))] \text{ and } \beta_{h}(V) = 0.5\exp(-0.025(V + 57)/18).$$

whereas the constants and time rate functions of our inhibitory neurons are (Börgers et al., 2008; Wang and Buzsáki, 1996):

$$C = 1, g_{Na} = 35, V_{Na} = 55, g_{K} = 9, V_{K} = -90, g_{L} = 0.1, \text{ and } V_{L} = -65, \text{ and } \alpha_{m}(V) = 0.1(V + 35)/[1 - \exp(-0.035(V + 35))], \beta_{m}(V) = 4\exp(-(V + 60)/18), \alpha_{n}(V) = 0.35\exp(-0.03(V + 58)/20), \beta_{n}(V) = 5/[1 + \exp(-(V + 52)/10)], \alpha_{h}(V) = 0.05(V + 34)/[1 - \exp(-0.03(V + 34)/10)], \beta_{h}(V) = 0.625\exp(0.01V + 44)/80).$$

The first subnetwork (i.e., the regulatory subnetwork) is driven at around 20 Hz, reflecting the oscillatory activity observed in electrophysiological data. The sensory subnetwork however is driven at around 40 Hz to roughly reflect the individual neurons’ firing rates. These oscillations were generated by applying a stationary heterogeneous external excitatory drive \(I_{app}\) to the excitatory cells, chosen from a Gaussian distribution with a variance of 0.05 and mean values 0.12 and 0.4, respectively.

Excitatory synaptic input to each neuron is modeled by a term of the form \(I_{syn} = g_{e}(V_{rev} - V)\sum_{i}\), where \(g_{e} = 0.0019/P_{Ny}\) is a Gaussian variable with the coefficient of variation 20%, and \(V_{rev} = 0\). The sum extends over those excitatory cells that send projections and the synaptic gating variable \(s\) is defined in the form (Palmigiano et al., 2017):

$$s = A \left( e^{-\frac{x - \delta_{0}}{\delta_{d}}} - e^{-\frac{x - \delta_{0}}{\delta_{d}}/2} \right)$$

where \(\delta_{0}\), \(\delta_{d}\) and \(A\) are the presynaptic spike time, synaptic delay and normalization factor respectively, and \(t = 3\) ms and \(t_{2} = 1\) ms determine the rise and decay synaptic time constants. Inhibitory synaptic input to each neuron is modeled by a term of the form \(I_{syn} = g_{i}(V_{rev} - V)\sum_{i}\), where \(g_{i} = 0.01/P_{Ny}\) is a Gaussian variable with a coefficient of variation 5%, and \(V_{rev} = -75\). The sum extends over those inhibitory cells that send projections and the synaptic gating variable \(s\) is the same as that for excitatory synaptic inputs, however here we have \(t = 4\) ms and \(t_{2} = 1\) ms.

The system of differential equations was solved in MATLAB using the midpoint method with time step \(\Delta t = 0.01\) ms. The system was initialized asynchronously (Börgers et al., 2005), i.e., we chose the initial state of neurons driven above their spiking threshold in a way that in the absence of synaptic currents, it will take each neuron a time span of \(\lambda T\) to fire its first spike, where \(T\) is the intrinsic spiking period and \(\lambda \epsilon [0, 1]\) is a uniformly-distributed random variable, and the remaining neurons (those driven below their spiking threshold) are initialized close to their stable state (on their phase plane). The system was solved for 500,000 steps (i.e., 5000 ms) and as a convention, spike times were taken to be the moments at which the membrane potential crosses \(-20\) mV from above. Here, we considered the population-averaged membrane potential as a heuristic of the collective neuronal activity, a computational analog of the LFP which is called LFP-like signal (Mazzoni et al., 2008; Palmigiano et al., 2017) and successfully captures the information content of the recorded LFP, although it fails to reproduce the recorded spectrum (Mazzoni et al., 2008).

To examine if there exists any systematic relationship between synaptic delay and the preferred phase of the spiking activity, we consid-
ered the synaptic delay \( d \) as a Gaussian-distributed random variable with a variance of 0.05 ms. We then increased its mean in the range of 0 to 1.5 ms by steps of 0.1 ms, carried out the simulation and finally calculated the preferred spiking phase of the pooled spike times of the sensory subnetwork relative to beta oscillations of the regulatory neuronal population (Fig. 7A).

CRedit authorship contribution statement

ST and ME designed the study; SBR and DK recorded the data; EA performed data analyses and computational modeling; EA, ST, and ME interpreted the data; and EA, FS, ST, and ME wrote the paper.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request. Data underlying the result figures are publicly available on figshare (https://doi.org/10.6084/m9.figshare.24129030).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.pneurobio.2023.102563.

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