

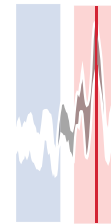
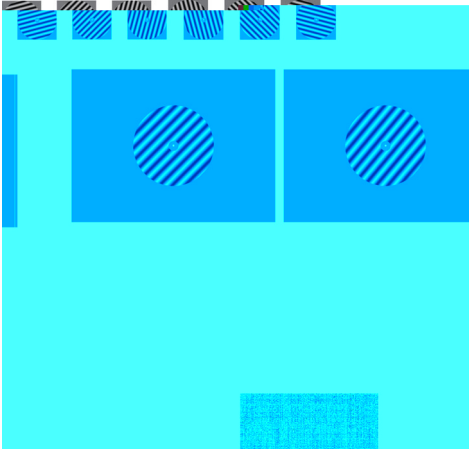
ARTICLE

Competing rhythmic neural representations of orientations during concurrent attention to multiple orientation features

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When a feature is attended, all locations containing this feature are enhanced throughout the visual field. However, how the brain concurrently attends to multiple features remains unknown and cannot be easily deduced from classical attention theories. Here, we recorded human magnetoencephalography signals when subjects concurrently attended to two spatially overlapping orientations. A time-resolved multivariate inverted encoding model was employed to track the ongoing temporal courses of the neural representations of the attended orientations. We show that the two orientation representations alternate with each other and undergo a theta-band (~4 Hz) rhythmic fluctuation over time. Similar temporal profiles are also revealed in the orientation discrimination performance. Computational modeling suggests a tuning competition process between the two neuronal populations that are selectively tuned to one of the attended orientations. Taken together, our

Attention, in addition to being able to dwell on certain



time period exhibited a flat profile ($F_{(5,84)} = 0.26$, $p = 0.93$, Supplementary Fig. 2a) with little representation of orientation information. Second, to investigate how the selection of the optimal orientation pattern by the SVM classifier might affect the outcome, we selected the surrogate optimal pattern as the instantaneous trial-wise vectors of sensor signals at the time point of the highest SVM decoding performance in the pre-stimulus period (baseline data), and performed the same IEM analysis. If our findings were somehow contingent on our approach of determining the optimal orientation pattern, rather than the orientation information itself, then one might expect a similar bell-shaped profile in the channel response function obtained from the surrogate optimal pattern. However, we did not observe such a profile in the channel response function for the post-stimulus period ($F_{(5,84)} = 0.59$, $p = 0.71$, Supplementary Fig. 2b).

Together, these results suggest that our findings are unlikely to arise by chance and could not be explained by the approach of selecting the optimal orientation pattern.

Neural representation of multiple attended orientations. Having validated the trained IEM based on the model training part data, we then used the IEM to reconstruct the time courses of orientation representations in the attention part when subjects concurrently attended to two orientation features (green box, Fig. 2a). In the attention part, subjects were presented with a multitude of sinusoidal gratings dispersed randomly. Half of the gratings were oriented at 45° while the others were oriented at 135° . An abrupt contrast increase with all the gratings of one orientation was introduced in each trial to presumably reset the

attentional process^{13,25}. So that we could examine the moment-by-moment neural representations of the orientation features with reference to a common temporal marker. Subjects were required to report a near-threshold orientation change (i.e., clockwise or anticlockwise) in the upcoming probe with respect to its closest orientation in the initial stimulus (Fig. 2a).

First, we examined whether the reconstruction results contained the information about the two attended orientations (45° and 135°). We calculated the channel response function for the 1000 ms post-cue period, by averaging the vectors of instantaneous channel responses across time points. Surprisingly, the channel response function showed a relatively flat pro

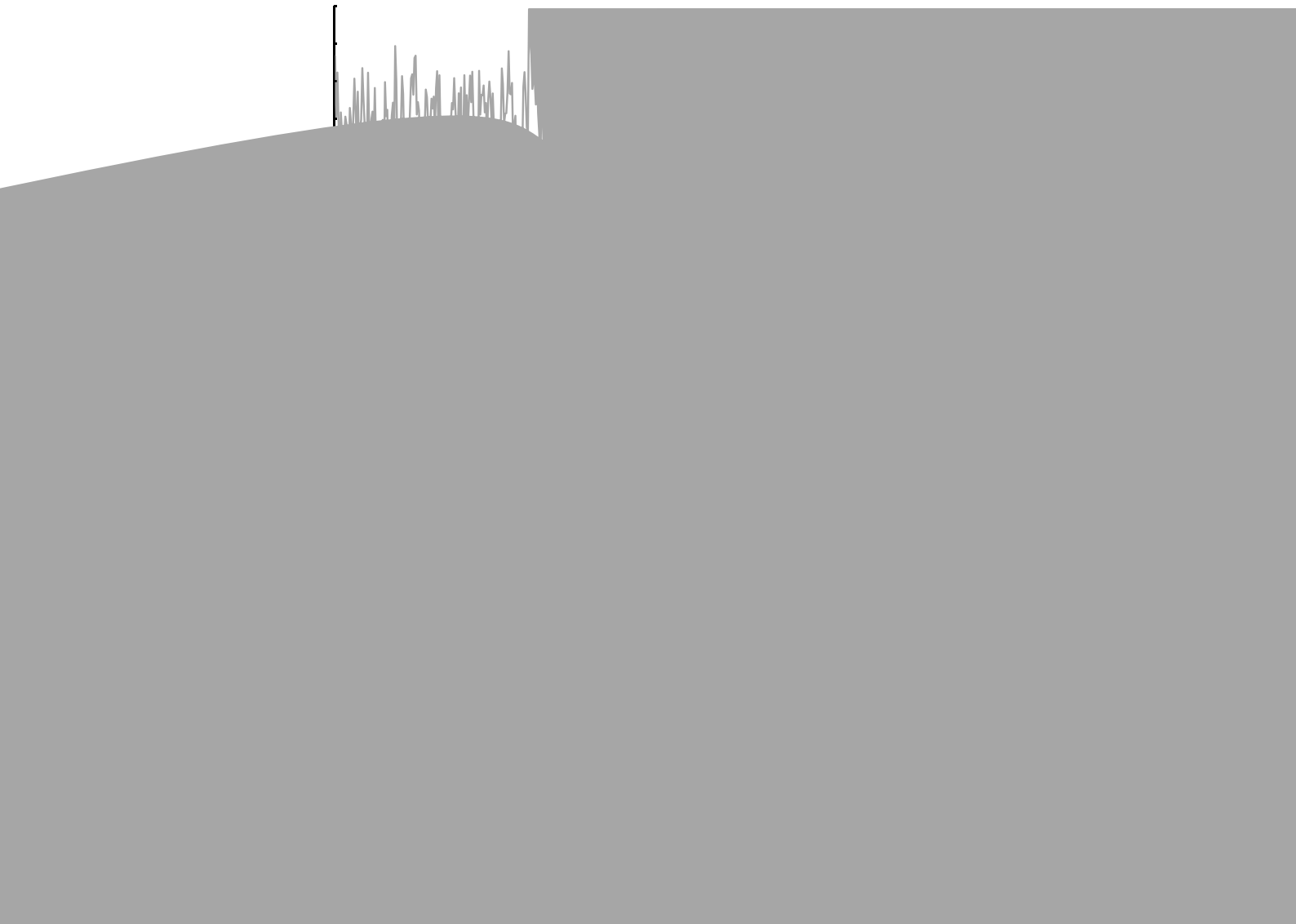
rhythmic fluctuating pattern. Moreover, the two orientation representations seemed to exhibit an alternating relationship such that the peaks of one coincided with the troughs of the other, and vice versa. Indeed, this time-resolved pattern was consistent with the flat time-averaged result (Fig. 2b). To examine the spectral contents of the orientation representation time courses, we performed a spectral analysis on the orientation representation fidelity time courses averaged across trials for each subject. The amplitude spectra were then averaged across subjects for each of the two orientations. As shown in Fig. 2d, both orientations showed a significant peak in the theta band (permutation test, corrected for multiple comparisons, $p < 0.05$; 45°: 3.75–4 Hz; 135°: 3.5–4 Hz). Thus, the temporal fluctuations of the two orientation representations were not stochastic but displayed a theta-band rhythmical pattern.

To further test the alternating relationship between the time courses of the two orientation representations, we calculated their phase difference in the theta-band for each subject. As shown Fig. 2e, the 45°–135° phase difference was not uniformly distributed across subjects, but was clustered around 164° (Rayleigh test for uniformity, $p < 0.001$) that was significantly different from 0° (Rayleigh test, $p < 0.001$) but not significantly different from 180° (Rayleigh test, $p = 0.16$), supporting their anti-phase relationship in the theta band. Therefore, the neural representations of the two concurrently attended orientations followed a rhythmically oscillating trajectory in which the enhancement of one feature representation was accompanied by the suppression of the other.

Behavioral oscillation in multi-orientation attention. Previous studies, by employing a time-resolved behavioral approach, have demonstrated neurophysiologically relevant rhythms in behavior^{10,11,13,14}. If multi-feature attention is indeed mediated by a rhythmic sampling neural mechanism, as suggested by our MEG results, we would expect a similar rhythmic profile in the time-resolved behavioral performance using the same multi-feature attention paradigm. We therefore employed the same stimuli and experimental procedure as those in the attention part of the MEG experiment, in combination with time-resolved psychophysics, to assess the temporal dynamics of multi-feature attentional process at the behavioral level. The only modification was the introduction of a systematically varied temporal lag between the cue and the probe (SOA), such that the probe appeared at one of 50 SOAs (50–1050 ms in steps of 20 ms) with equal probability.

Figure 2f illustrates the orientation discrimination accuracy as a function of cue-to-probe SOA for the 45° (red) and the 135° (blue) orientations, respectively. The behavioral results showed a fluctuating temporal profile as well as an alternation between the two orientations. We then applied the same statistical procedure as that used for the MEG data to the time-resolved behavioral data, and identified a significant theta-band spectral peak (permutation test, corrected for multiple comparisons; 45°: 3.75–4.5 Hz, $p < 0.025$; 135°: 3.75–4.25 Hz, $p < 0.025$) for both orientations (Fig. 2g). Moreover, sensitivity to the two orientation features exhibited an anti-phase relationship in the theta band (Rayleigh test for uniformity,

orientations Fig.idg.Tg..hroveJNotablyT]tipleone



(i.e., ~4 Hz), thus suggesting similar mechanisms mediating the two attention forms.

Our findings, from both MEG recording and behavioral measurement, consistently show that attention to multiple features is coordinated at a theta-band rhythm, a rhythm known to implement attentional allocation among multiple locations^{11,13,14,25,34,35}. In addition to attention, theta-band rhythm is also known to be involved in other cognitive functions that deal with multiple items simultaneously. For example, it was found that sustained theta-band power during the delay period in working memory tasks³⁶ could predict subsequent retrieval performance³⁷. By phase-modulating the gamma-band power, the theta-band rhythm served a critical function in disambiguating individual items held in working memory³⁸ and encoding their relationships³⁹. Therefore, theta-band rhythm might act as a functional bridge that connects a cascade of cognitive processes⁴⁰, including information selection, representation, storage, and readout, with external behaviors. Functionally, this ubiquitous temporal code is utilized to facilitate the information exchange and coordination between different brain regions that are involved in these cognitive processes⁴¹, and helps to enhance processing capacity in attention and memory^{42,43}.

Previous studies have shown that when a single feature is attended, tuning curves of individual neurons were shifted towards the attended feature^{8,26}, thus consistent with the TS model. Interestingly, our modeling results instead support the TC model over the TS model. One possible explanation is that the two mechanisms are optimal under different circumstances. Tuning shift could maximize the sensitivity to the attended feature⁴ during uni-feature attention but would be suboptimal for multi-feature attention because it would be highly inefficient to shift the tunings of almost all neuronal populations every hundreds of milliseconds. In contrast, tuning competition would be more advantageous in implementing the rhythmic sampling process, as it relies on concurrent tuning changes of particular neuronal populations without necessarily involving other neuronal populations⁴⁴. Importantly, we identified rhythmic sharpening and widening of the tuning curves in our modeling at the same theta-band frequency as in the temporal dynamics of the feature representation and behavioral performance. This observation echoes previous findings of attention-induced selectivity increase in visual cortical neurons representing the attended object⁴⁵ or lower-level features⁴⁶. Feature information encoded in neuronal responses is critically constrained by the slope of neuronal tuning curves. Sharpening of a tuning curve increases its slope, which in turn improves the quality of neuronal code and the behavioral discrimination performance⁴⁷. While our modeling results were consistent with previous findings that directing attention to basic visual features, such as color and motion, influences the selectivity of individual neurons^{48–51}, given the limited spatial resolution of MEG technique, we cannot assert that the tuning competition occurs at the single-neuron level. It could also occur at the population response level. In fact, tuning width changes at the population level do not necessarily arise from tuning width (or selectivity) changes at the single-neuron level, since a population tuning curve could be affected by changes in amplitudes (or gains) of individual neuronal tuning curves without necessarily changing the shapes (or widths) of the tuning curves⁴⁹.

Although our results are based on neuromagnetic signals from occipital sensors, it is unlikely that our findings only reflect localized neuronal processing in visual cortex. Feature-based attention is known to recruit a large-scale network of brain regions, including V4, frontal eye field (FEF) and ventral prearcuate gyrus (VPA)^{3,52}. In specific, it was found that feature-based attention signals arise earlier in VPA than V4, suggesting that the source of feature selection signals might be located outside the visual system³. Hence, the rhythmic attentional sampling in the feature space might reflect a dynamic interplay between occipital cortex and higher-order

attention-related regions^{34,35}. In different phases of a theta-band cycle, top-down signals bias the local competition between feature-selective neurons in visual cortex towards one feature over the other. Consequently, local neuronal computations are temporally orchestrated by higher-order regions, achieving a time-multiplexing representation.

It has recently been proposed that IEM outputs could not be used to infer changes in tuning properties at the single-neuron level, as the IEM outputs were only determined up to a linear transform and thus the recovered model responses are only one of an infinite family of equivalent solutions⁵³. However, we believe that these arguments do not speak against the validity of our approach or our findings. While the IEM approach might not be able to provide insights into the tuning properties at the single-neuron level, it does provide an effective way to assay neural representations at the neuronal population level⁵⁴, which enabled us to reveal the rhythmic changes in orientation representations in theta-band. It should be emphasized that here we did not seek to establish a direct link between single-neuron level tuning and population-level representation based on our current findings, though this issue should be investigated in the future.

In summary, we found, for the first time, that multi-feature attention is mediated by a rhythm-based, time-multiplexing neural machinery that sampled each attended feature periodically at theta band. Moreover, the rhythmicity might be implemented by a tuning competition process between the neuronal populations selective to the attended features.

Methods

Participants. A total of 30 students (13 males, 18–25 years old) were recruited from Peking University. Fifteen of them (7 males) participated in the MEG experiment and the rest participated in the behavioral experiment. All subjects were naive to the purpose of the study. They were right-handed, reported normal or corrected-to-normal vision, and had no known neurological or visual disorders. Written informed consents were collected from them before the experiments. Experimental procedures were approved by the human subject review committee at Peking University.

Stimuli and task. The MEG experiment had two parts—the model training part and the attention part. In the model training part, the visual stimulus was an annulus of sinusoidal grating (inner radius = 1.5°, outer radius = 12°, spatial frequency = 0.225 cycles per degree, Michelson contrast = 1, mean luminance = 80 cd/m²) centered at fixation. Its phase was randomized and its orientation could be one of six possible orientations from 15° to 165° in steps of 30°. In each trial, the grating stimulus was displayed for 1000–1250 ms, and was then slightly rotated for 150 ms. Subjects indicated the direction of the rotation (clockwise or counterclockwise) (Fig. 1a).

In the attention part, the stimulus consisted of two arrays of phase-randomized sinusoidal gratings (radius = 0.3°, spatial frequency = 3.8 cycles per degree, Michelson contrast = 0.8) oriented at ~45° and ~135°, which were presented in an invisible 9 × 9 rectangular grid centered at fixation. Gratings in the same array shared identical orientation. The size of the grid was 12° × 12°. Spatial randomization of the gratings proceeded in two steps. In the first step, 28 grid cells were randomly selected as the candidate locations for the gratings. In the second step, the location of each grating center was further jittered within the grid cell. The aim of the two-step manipulation was to conceal the spatial configuration of the grid and to discourage subjects from predicting the locations of the gratings, such that subjects' attention would be directed to both orientation features that were spatially interleaved throughout the grid. Similar to Herrmann et al.¹⁸, the nine grid cells closest to fixation were intentionally left out such that subjects needed to distribute their attention throughout the grid instead of biasing towards the innermost locations. Each trial started with a 300 ms fixation point. Then the two grating arrays were presented for a random duration between 500 and 1000 ms to minimize potential expectation effects of an upcoming resetting cue. The resetting cue was a 200 ms contrast increment ($\Delta = 0.2$), which could presumably reset the attentional process such that we could examine the moment-by-moment neural representations of the orientation features with reference to a common temporal marker. Similar resetting cues have been employed in previous studies to investigate the temporal dynamics in multi-target attention^{10,12–14}. It is important to note that the contrast increment occurred with all gratings in one array rather than in a discrete location. After resetting, the two grating arrays remained on the screen for 1000–1250 ms before they were replaced by a 100 ms probe comprising the same number of gratings oriented at approximately either 45° (right tilted probe) or 135° (left tilted probe). Subjects were fully aware of the cue validity (50%) before the experiment, i.e., in half of the trials the probe orientation was

approximately parallel to the cued orientation while in the other trials the probe orientation was approximately perpendicular to the cued orientation. Gratings in the probe went through the same two-step spatial randomization process as described above to minimize location-based selection effects.

Subjects indicated whether the probe orientation was clockwise or counterclockwise of its closest orientation in the two grating arrays. To prevent subjects from holding a reference of the two orientations in memory and using the reference for the task, we randomly introduced a small orientation jitter ($\pm 3^\circ$) in some trials as in Herrmann et al.¹⁸ such that the observers were uninformative as to which orientations ($42^\circ/138^\circ$, $45^\circ/135^\circ$, or $48^\circ/132^\circ$) would be presented in a trial. Hence, subjects had to attend to the two orientations in each trial in order to complete the task. Inter-trial interval varied randomly between 1000 and 1500 ms. Subjects underwent a total of five blocks for the model training part and eight blocks for the attention part in an interleaved order. Each model training block contained 72 trials (12 for each of the 6 orientations) and each attention block contained 60 trials (30 for each probe condition). Trial order was randomized in all blocks. A two-up-one-down staircase procedure was used in each block to match task difficulty across subjects.

MEG signal acquisition. Neuromagnetic signals were recorded continuously with a 306-channel (204 planar gradiometers, 102 magnetometers), whole-head MEG system (Elekta Neuromag TRIUX) in a magnetically shielded room. Raw MEG data were offline band-pass filtered between 0.1 and 35 Hz, resampled to 250 Hz, and baseline corrected using Fieldtrip⁵⁵ before subsequent data analysis.

Optimal orientation pattern localization. For each subject, time-resolved orientation decoding analysis was conducted on the data from the model training part using linear supporting vector machine (libSVM) to localize the optimal orientation pattern. The optimal orientation pattern was defined as the MEG signals that contained the largest amount of orientation information, i.e., the trial-wise vectors of sensor responses that achieved the highest decoding accuracy. Seventy-two sensors covering the occipital lobe that were labeled as Occipital in the MEG data acquisition system were selected for data analyses²⁴. Because orientation selectivity is relatively weaker in higher-order brain regions⁵⁶, inclusion of signals from these regions might introduce additional noise. For each time point (from 250 ms before to 1250 ms after stimulus onset), MEG data were arranged in the form of 360×72 matrix comprising 360 trial-wise vectors of sensor signals (60 for each orientation category). A six-way decoder was trained to classify these vectors into one of six orientation categories using a leave-one-block-out cross-validation procedure, yielding a decoding accuracy time course for each subject. We extracted the trial-wise vectors of instantaneous sensor signals at the time point with the highest decoding accuracy, which formed the optimal orientation pattern (Fig. 1d). This pattern was then used to train the IEM.

Reconstruction of the time-resolved orientation representation. According to the assumptions of IEM, instantaneous sensor responses at a single time point across trials could be expressed as a linear combination of the responses of six orientation channels (from 15° to 165° in steps of 30°):

$$\mathbf{B} = \mathbf{W}\mathbf{C}, \quad (1)$$

where \mathbf{B} is the matrix of sensor signals at a given time point (72 sensors-by- N trials), \mathbf{W} is the matrix of linear weights for the orientation channels (72 sensors-by-6 channels), and \mathbf{C} is the matrix of channel responses (6 channels-by- N trials). The IEM analysis involved two stages: model training and model-based reconstruction. In the model training stage, the mapping from the MEG sensor signals to the six orientation channel outputs (i.e., \mathbf{W}) was estimated using the optimal orientation pattern that carried the richest orientation information. To this end, we modeled the idealized tuning in each orientation channel as the half-sinusoidal function raised to the fourth power peaked at the channel's preferred orientation⁵⁷ (Fig. 1b). Hence, for each trial in the model training sessions, the channel responses could be predicted from these idealized tuning functions (Fig. 1c). Based on the predicted channel responses, the weight matrix \mathbf{W} could be estimated as

$$\hat{\mathbf{W}} = \mathbf{B}_1 \mathbf{C}_1^T (\mathbf{C}_1 \mathbf{C}_1^T)^{-1}, \quad (2)$$

where \mathbf{B}_1 (72 sensors-by-360 trials) is the optimal orientation pattern matrix obtained as described in the previous section, and \mathbf{C}_1 (6 channels-by-360 trials) is the matrix of predicted channel responses for the presented orientation in each trial, which was obtained from the idealized channel tuning functions. It is important to note that estimation of \mathbf{W} involved only the model training part data and that the mapping was assumed to be invariant across the model training part data and the attention part data. In the model-based reconstruction stage, the weight matrix was then applied to the instantaneous sensor signals in the attention part data (i.e., \mathbf{B}_2) at each time point to estimate the instantaneous individual channel responses:

$$\mathbf{C}_2 = (\hat{\mathbf{W}}^T \hat{\mathbf{W}})^{-1} \hat{\mathbf{W}}^T \mathbf{B}_2, \quad (3)$$

where \mathbf{B}_2 (72 sensors-by-480 trials) is the matrix of instantaneous sensor signals in the attention part data and \mathbf{C}_2 (6 channels-by-480 trials) is the matrix comprising

column vectors of estimated trial-wise channel responses. These trial-wise vectors were then averaged, yielding one vector of channel responses for each time point (Fig. 1e). Hence, the orientation information in each trial is represented in the channel space. To quantify to what extent the channel responses encode the information of a given orientation, we computed the representational fidelity metric as a mean of six unit vectors pointing in the polar angle directions corresponding to the channels' preferred orientations and weighted by the estimated channel responses²¹

$$\bar{\mathbf{z}} = \frac{\sum_k c_k \bar{\mathbf{u}}_k}{6}, \quad k = 1, 2, \dots, 6, \quad (4)$$

where $\bar{\mathbf{z}}$ is the resultant mean vector, c_k is the response of the k th channel, and $\bar{\mathbf{u}}_k$ is its corresponding unit vector. This mean vector was then projected onto a unit vector pointing in the polar angle direction along the orientation of interest (the six orientations in the model training part, 45° and 135° in the attention part),

$$R = |\bar{\mathbf{z}}| \cos \phi, \quad (5)$$

where ϕ is the angle between the mean vector and the polar angle direction along the orientation of interest. The resultant value R hence provide a quantitative measure of the extent to which the information of a given orientation was encoded in the channel responses, with a greater R value above zero indicating a stronger representation of the orientation of interest (Fig. 1f). Using this approach, we calculated the representation fidelity of the orientation of interest at each time point (Fig. 1g), which yielded the orientation representation fidelity time course. For the attention part data, we epoched the representation fidelity time courses from 0 to 1000 ms after the onset of the resetting cue, removed the linear trends of these epochs and performed spectral analysis using Fast Fourier Transform (FFT). spondinis time

orientation of the population response profile, which, according to the model hypothesis, would rhythmically shift between 45° and 135°. The tuning competition model was defined as the weighted sum of two exponentiated cosine functions that characterized the tuning of the neuronal populations selective to the two attended orientations (i.e., 45° and 135°):

$$f(x|A_1, K_1, A_2, K_2, b) = A_1 e^{K_1 \{\cos(\frac{\pi}{4}-x)\}-1} + A_2 e^{K_2 \{\cos(\frac{3\pi}{4}-x)\}-1} + b, \quad (7)$$

where A_1 , K_1 , A_2 , and K_2 denote the amplitude and the concentration of the two tuning curves. For both models, parameters were varied to obtain the minimal sum of squared errors between the population response profile and the model prediction. To statistically compare the two models, we computed the root mean squared deviation (RMSD) of the two fitted models for each time point:

$$\text{RMSD} = \sqrt{\text{SSE}/(N-k)}, \quad (8)$$

where SSE is the sum of squared errors. N is the number of data points (i.e., 180), and k is the number of model parameters. For each subject and each model, we calculated the mean RMSD by averaging the model's RMSD values across all time points. A non-parametric Wilcoxon's signed rank test was conducted to compare the RMSD values of the two models across subjects.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data supporting the findings of this study are available from the corresponding authors upon request.

Code availability

Codes associated with the findings of this study are available from the corresponding authors upon request.

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