Dual-format attentional template during preparation in human visual cortex

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Abstract

Goal-directed attention relies on forming internal templates of key information relevant for guiding behavior, particularly when preparing for upcoming sensory inputs. However, evidence on how these attentional templates is represented during preparation remains controversial. Here, we combine functional magnetic resonance imaging (fMRI) with an orientation cueing task to isolate preparatory activity from stimulus-evoked responses. Using multivariate pattern analysis, we found decodable information of the to-be-attended orientation during preparation; yet preparatory activity patterns were different from those evoked when actual orientations were perceived. When perturbing the neural activity by means of a visual impulse ('pinging' technique), the preparatory activity patterns in visual cortex resembled those associated with perceiving these orientations. The observed differential patterns with and without the impulse perturbation suggest a predominantly non-sensory format and a latent, sensory-like format of representation during preparation. Furthermore, the emergence of the sensory-like template coincided with enhanced information connectivity between V1 and frontoparietal areas and was associated with improved behavioral performance. By engaging this dual-format mechanism during preparation, the brain is able to encode both abstract, non-sensory information and more detailed, sensory information, potentially providing advantages for adaptive attentional control. For example, consistent with recent theories of visual search, a predominantly non-sensory template can support the initial guidance and a latent sensory-like format can support prospective stimulus processing.

Keywords

Attentional selection, representational format, fMRI, decoding, visual cortex, impulse perturbation

Introduction

To address the challenge of processing the overwhelming amounts of sensory inputs from the external environment, the brain must allocate attentional resources to prioritize the processing of task-relevant information. Importantly, humans can proactively prepare for stimulus selection before the arrival of sensory inputs (Summerfield & De Lange, 2014) . For example, when preparing to hail a taxi on the road, we tend to form a mental representation of the defining features of a taxi (e.g., yellow with a car-like shape). This ability relies on the formation of attentional templates — mental representations of the target — to accelerate stimulus selection and resolve perceptual competition by enhancing task-relevant information and suppressing irrelevant information (Desimone & Duncan, 1995; Kastner et al., 1999). While most attentional models posit that attentional templates during stimulus processing reflect veridical representations of the target (Jigo et al., 2018; Malcolm & Henderson, 2009), the nature of the template during preparation remains less understood.

A classical view suggests that attentional template during preparation may reflect veridical target features, analogous to the representational format during stimulus selection. However, evidence supporting this account has been mixed. For example, while some previous fMRI studies have demonstrated that preparatory activity contains target information similar to the sensory responses to the corresponding targets (Kok et al., 2014; Lewis-Peacock et al., 2015; Stokes et al., 2009), more recent electrophysiological studies suggest that, if anything, this template is engaged only shortly before the expected arrival of sensory input rather than being continuously active (Grubert & Eimer, 2018; Myers et al., 2015). Notably, in some cases the template is even largely undetectable during preparation (Wen et al., 2019). Alternatively, an emerging view suggests a non-veridical template suffices for guiding attention during preparation, where precise processing of stimuli may be unnecessary at this stage. Support for this notion comes from the identification of attentional signals during preparation that differ from neural signals observed during perceptual target processing (Gong et al., 2022). Recent theories of visual search also propose a non-veridical, “good-enough”

template for early attentional guidance (Wolfe, 2021; Yu et al., 2023). However, it remains unclear whether a "good-enough" template for search also applies to preparatory attention.

The notion that there may be a sensory and non-sensory attentional template might not be as far-fetched as it seems. Indeed, it is feasible that during preparation, following stimulus presentation, attentional signals undergo a transformation from a non-sensory to a sensory-like template. Previous behavioral (Hamblin-Frohman & Becker, 2021; Yu et al., 2022) and neural studies (Gong et al., 2022; Jigo et al., 2018; Wen et al., 2019) are generally consistent with this idea of coarse-to-fine transitions, suggesting that during preparation, a sensory-like template may not be initially necessary but only becomes relevant when the stimulus needs to be identified. However, if and in what way the brain coordinates these non-sensory and sensory-like templates remains unclear. Here, we propose that during preparation, a sensory-like template may be stored in a latent (e.g., activity-silent) state concurrently with a non-sensory template. This idea parallels recent findings from working memory studies, which suggest that information intended for proactive use is kept in activity-silent traces to support future behavior (Stokes, 2015; Wolff et al., 2015, 2017). The present study seeks to determine the possibility of the latent, sensory-like template during the preparation for discriminating an upcoming stimulus.

To test these hypotheses, participants engaged in a cuing task in which they prepared during an extended period of time for the presentation of a compound stimulus grating containing the cued orientation and a distractor orientation. In addition, in order to be able to construct the sensory-format representations (leftward and rightward orientation), single orientations were presented during the perception task. Critically, we used a "pinging" technique combined with multivariate decoding methods, which has been shown to be effective in retrieving information from latent brain states (Duncan et al., 2023; Wolff et al., 2015, 2017; Zhang & Luo, 2023). In the standard condition (*No-Ping session*), the preparation period was devoid of visual impulses. During preparation, the neural activity patterns in visual and frontoparietal areas could discriminate between the orientations that participants were preparing for. Yet, neural activity patterns evoked by the perception of orientations were distinct from those evoked during preparation for upcoming orientations, suggesting a predominantly non-sensory template during preparation. By contrast,

when we presented a high-contrast, task-irrelevant impulse stimulus during preparation (*Ping session*), neural activity patterns evoked by the perception of orientations were similar to those activated by the preparation for orientations in the visual cortex, suggesting the existence of a latent, sensory-like format of representation during preparatory attention. Furthermore, the emergence of sensory-like template coincided with enhanced information connectivity between V1 and frontoparietal areas and was associated with improved behavioral performance. Our findings provide evidence for the co-existence of two formats of attentional templates (non-sensory vs. sensory-like) during preparation, as well as a novel neural mechanism for their maintenance in different functional states (active vs. latent). We propose that this dual-format representation may serve to increase flexibility of attentional control.

Results

Behavioral performance during the attention tasks

In an orientation cueing task, participants were shown a color cue indicating the reference orientation (45° or 135°) to attend to during preparation period (a delay of 5.5 s or 7.5 s) with or without the impulse perturbation (Fig 1A). This was followed by the presentation of a compound stimulus consisting of two oriented gratings. During the stimulus selection period (after the gratings appeared), participants were tasked with discriminating a small angular offset of the cued grating from the cued reference orientation. The angular offset was individually thresholded before the scanning sessions (mean offset = 2.50° in the No-Ping session and 2.52° in the Ping session) without significant difference between two sessions (independent t-test: $t(19) = 0.085$, $p = 0.932$, Cohen's d = -0.027). Participants' discrimination performance showed no significant difference between two attended orientations in either the No-Ping (paired t-test: $t(19) = 1.439$, $p = 0.166$, Cohen's d = -0.321) or the Ping session (paired t-test: $t(19) = 0.494$, $p = 0.627$, Cohen's d = 0.122; Fig 1C). A two-way mixed ANOVA (attended orientation × session) revealed neither significant main effects (attended orientation: $F(1,38) = 0.392$, $p = 0.535$, $\eta_p^2 = 0.01$; session: $F(1,38) = 0.001$, $p = 0.970$, $\eta_p^2 < 0.001$) nor interaction effect ($F(1,38) = 1.811$, $p = 0.186$, $\eta_p^2 = 0.045$). Bayesian

analyses provided moderate evidence to support the null hypothesis ($BF_{excl} > 3.633$), suggesting comparable performance levels between two sessions and two attended orientations.

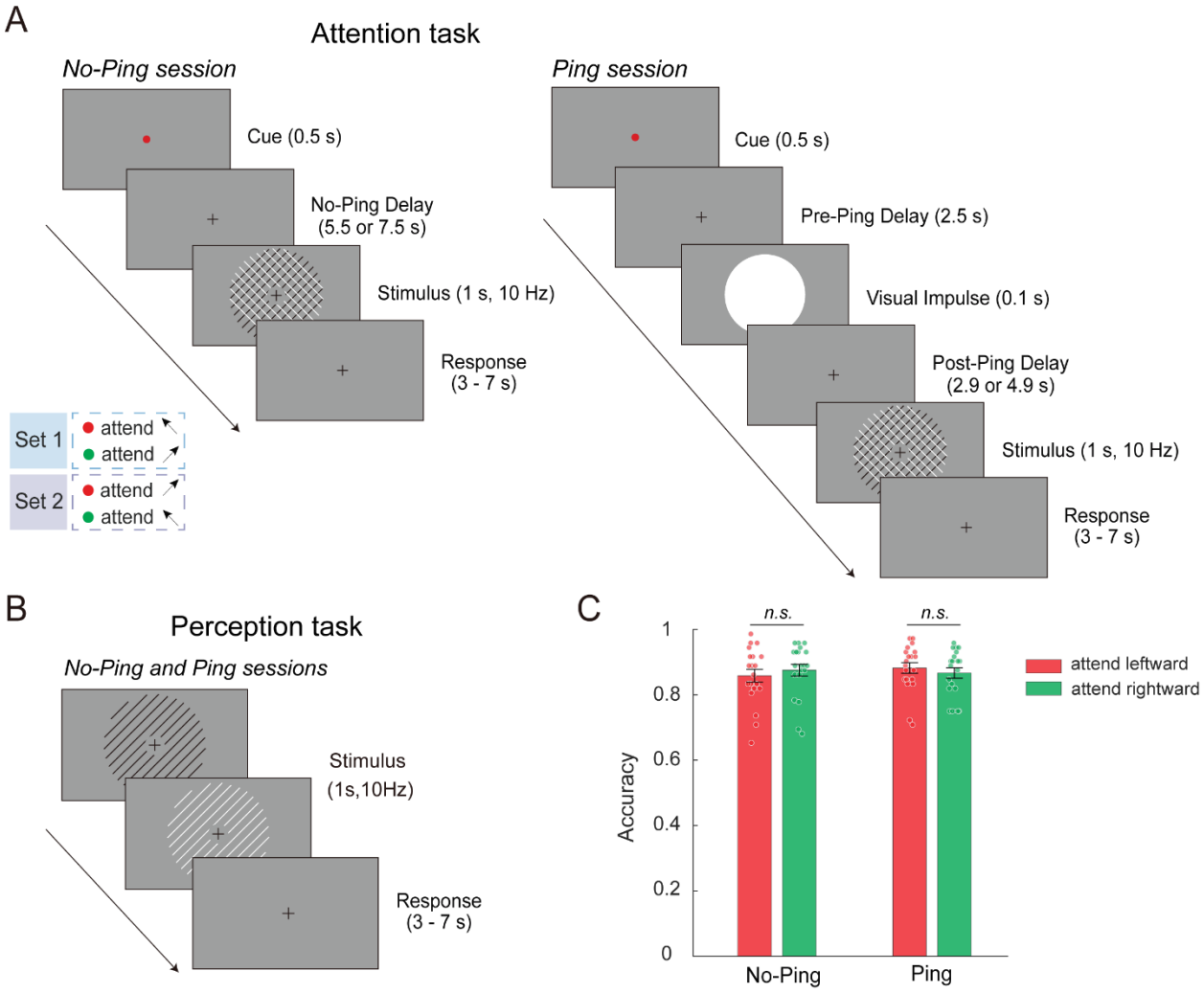

Fig 1. Experiment procedure and behavioral performance. (A) Attention tasks in the No-Ping and Ping sessions. Note that only long-delay trials are shown. A small proportion of short-delay trials (20%, with a delay of 1.5 s or 3.5 s) were included to create temporal uncertainty and encourage consistent active preparation during the delay. Both component gratings were flickering at 10 Hz between white and black, so that luminance could not confound either the task strategy (e.g., attending to luminance) or neural measures. The inset shows two sets of color-orientation mapping, which were reversed halfway through the experiment to minimize the impact of cue-induced sensory difference on neural activity. A high-contrast impulse was presented during preparation period in the Ping session. (B) Perception task. Similar to the attention task, the single-orientation grating also flickered at 10 Hz between white and

black. (C) Behavioral accuracy in the attention tasks in the No-Ping and Ping sessions. Each dot represents one subject's data. Error bars denote standard error of the means (SEM).

A default, non-sensory representation of attentional template during preparation

The first aim of this study was to determine whether attentional signals during preparation are encoded in a sensory-like or non-sensory format. To address this, we first examined whether, in the attention task during the No-Ping condition, the distributed neural pattern contained feature-specific information. We trained and tested separate classifiers to predict the attended orientation during the preparation and stimulus selection periods (Fig 2A, "Attention decoding"; see Materials and Methods for details). This analysis was performed for each of the four regions along the visual hierarchy, including primary visual cortex (V1), extrastriate visual cortex (EVC), intraparietal sulcus (IPS) and prefrontal cortex (PFC). The average decoding accuracies for both preparation and stimulus selection periods were significantly above chance level in each region (Permutation analyses: $ps < 0.004$ across regions, Fig 2B), indicating that the brain maintained reliable information about the attended feature both before and after the onset of the compound grating. Next, we examined whether the preparatory activity reflected a sensory-like format of attentional template (Fig 2A, "Cross-task generalization", see Materials and Methods). We trained a classifier using data from the perception task (leftward vs. rightward orientation; Fig 1B) and tested its performance on data from the preparation period in the attention task (attend leftward vs. attend rightward). However, this cross-task generalization analysis yielded no significant effects ($ps > 0.132$ across the regions). In contrast, we observed above-chance generalization from the perception task to the stimulus selection period ($ps < 0.001$ across regions, Fig 2C), confirming previous findings of the sensory-like attentional template following stimulus presentation (Gong et al., 2022; Jigo et al., 2018; Wen et al., 2019).

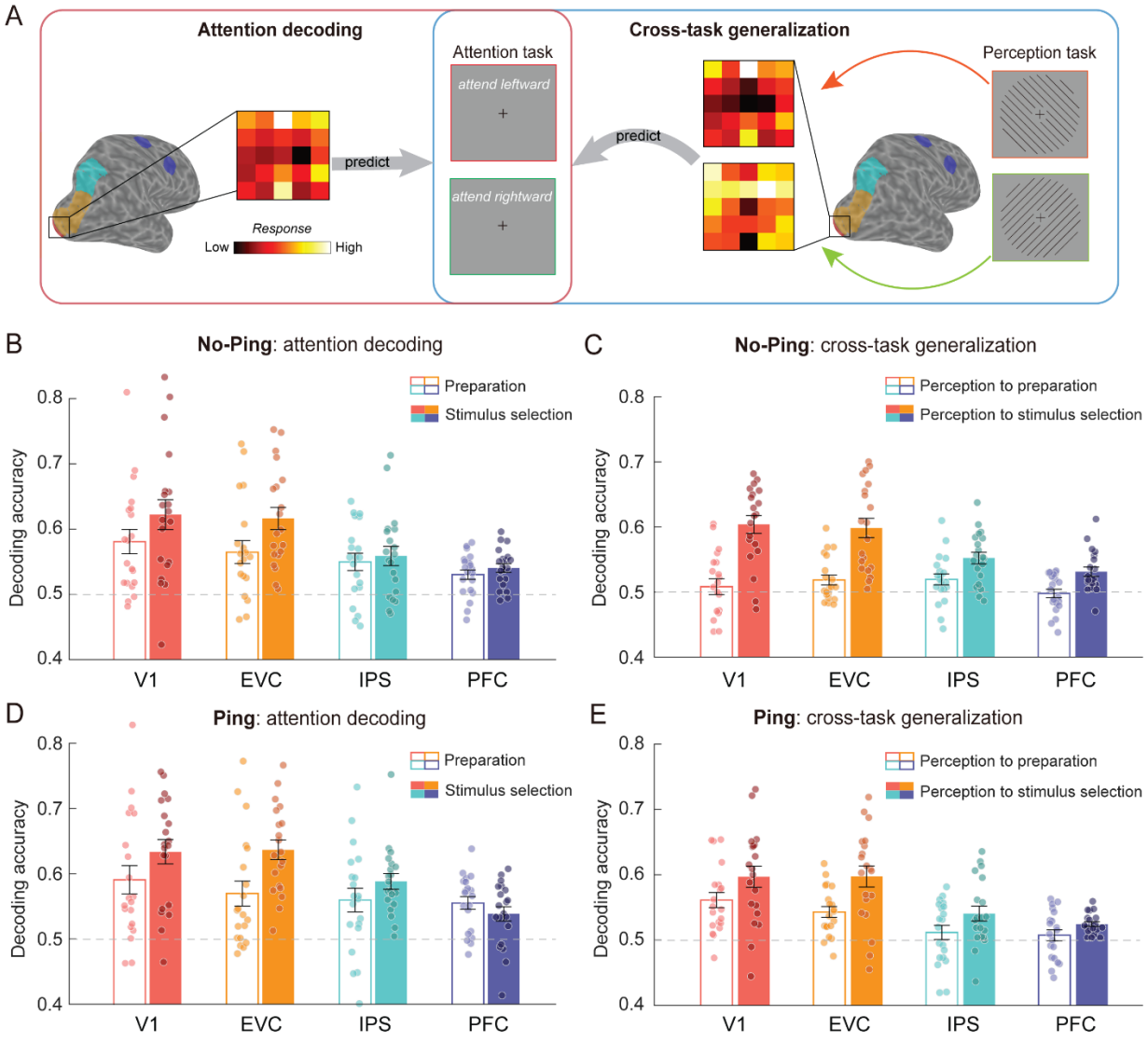

Fig 2. MVPA for the No-Ping session and Ping session. (A) Schematic illustration of the decoding of attended orientation (attend leftward vs. attend rightward) in the attention task (left panel) and the cross-task generalization analysis from perception task to the attention task (right panel). The four regions are shown on a representative right hemisphere as colored areas: V1 is marked in red, EVC in yellow, IPS in cyan and PFC in purple. (B) Decoding accuracy during preparation and stimulus selection periods across regions in the No-Ping and (D) Ping session. (C) Cross-task generalization performance from the perception task to the preparatory periods and the stimulus selection periods across regions in the No-Ping and (E) Ping session. The dashed lines represent the theoretical chance level (0.5). Each dot represents one subject's data. Error bars denote SEM.

Before drawing conclusions based on the lack of generalization from the perception task to preparatory attention, we considered two alternative explanations to rule out potential confounds. First, the robust attention decoding during preparation ruled out the possibility that participants were not actively engaged in the task during preparation (Fig 2B, unfilled bars). Second, the generalizable effect from the perception task to the stimulus selection period across regions (Fig 2C, filled bars) argues against the possibility of low statistical power. Overall, these findings suggest that the preparatory attention and sensory processing of features have distinct formats, presumably reflecting a non-sensory format of representation during the preparation. These results replicate those of a previous fMRI study using motion stimuli with a similar design (Gong et al., 2022). Furthermore, consistent with previous studies (Gong et al., 2022; Jigo et al., 2018), univariate analysis did not reveal any reliable difference in overall BOLD responses between attention orientations (Supplementary Information and S1 Fig).

A latent, sensory-like attentional template during preparation revealed by visual impulse

The second aim of our study was to examine whether a latent, sensory-like template exists during preparation. While this precise template may not be necessary for preparation, it is relevant for subsequent target selection and discrimination (i.e., select the cued grating from the compound stimulus and discriminate a small angular offset between the cued grating and the reference orientation). To test this hypothesis, we perturbed the neural activity by means of a visual impulse during the preparation period in the Ping session (Fig 1A, right panel). Using the same analyses as those performed in the No-Ping session, robust attentional signals were observed during both preparation and stimulus selection periods (Permutation analyses: $ps < 0.001$ across regions; Fig 2D). Importantly, the cross-task generalization analyses indicated that the visual impulse led to above-chance generalization from the perception task to preparation period (Fig 2E, unfilled bars) in V1 and EVC ($ps < 0.001$), but not in IPS and PFC ($ps > 0.584$), along with generalizable effects from the perception task to the stimulus selection periods ($ps < 0.036$ across regions; Fig 2E; filled bars). These results suggest that different brain areas are involved in coding for sensory-like templates. To further evaluate whether the cross-task generalization from the perception task

188 to the preparation period was statistically different with and without visual impulse, we conducted a two-
189 way mixed ANOVA (session × region) on the generalization performance. The analysis revealed main
190 effects of region ($F(3,114) = 5.220$, $p = 0.002$, $\eta_p^2 = 0.121$), session ($F(1,38) = 7.321$, $p = 0.010$, $\eta_p^2 = 0.162$),
191 and importantly, a significant interaction effect ($F(3,114) = 3.964$, $p = 0.010$, $\eta_p^2 = 0.094$), supporting the
192 observation that the visual impulse led to significantly increased decoding accuracy in V1 (independent t-
193 test: $t(38) = 3.145$, $p = 0.003$, Cohen's d = 0.995) and EVC (independent t-test: $t(38) = 2.153$, $p = 0.038$,
194 Cohen's d = 0.681), but not in the frontoparietal regions (*ps* > 0.374). This dissociable result between the
195 two sessions further supports the activation of a latent, sensory-like template by the visual impulse during
196 preparatory attention.

197 To further solidify this conclusion, following analyses were used to examine several alternative
198 possibilities. First, we examined whether the impulse-driven generalization resulted from stronger feature
199 information in the Ping compared to No-Ping session during the perception task. This was not the case, as
200 evidenced by comparable levels of decodable orientation information between the Ping and No-Ping
201 sessions (see Supplementary Information and S2 Fig). Next, we asked whether the increased generalization
202 was due to generally stronger attentional signals in the Ping session during the attention tasks – for example,
203 if visual impulses simply refocused attention during long delays. This was not the case, as the two-way
204 mixed ANOVAs (session × region) on attention decoding accuracy revealed neither a significant main
205 effect of session nor an interaction effect during both the preparation (*ps* > 0.519; $BF_{excl} > 3.247$) and
206 stimulus selection periods (*ps* > 0.336; $BF_{excl} > 3.297$), suggesting comparable amount of attentional
207 information between the two sessions. Therefore, the findings of impulse-driven sensory-like template in
208 the visual cortex during preparation cannot be explained by general differences between two sessions.
209

210 **Matching preparatory attention to sensory template: impact on neural representation and**
211 **behavior**

212 The reported decoding accuracy from the cross-task generalization analysis quantifies the degree to which
213 differences in neural activity pattern between two conditions are shared across attention and perception

214 tasks. However, it does not directly measure how similar the neural patterns are when attending to an
215 orientation compared to perceiving that orientation. Unlike decoding accuracies, Mahalanobis distance
216 provides a continuous measure for characterizing representational geometries between different conditions
217 (Mahalanobis, 1936). To further corroborate our findings of the impulse-driven sensory-like template, we
218 calculated the Mahalanobis distance between each attention condition during preparation and each
219 perception condition (see Materials and Methods). If the patterns of activity reflect a sensory-like template,
220 we would expect greater pattern similarity (smaller distance) between "attend leftward" and "perceive
221 leftward" than between "attend leftward" and "perceive rightward", and vice versa for the "attend rightward"
222 conditions (see Fig 3A for a schematic of the four pair-wise distance measures), leading to an interaction
223 between attended and perceived orientation conditions.

224 We used a two-way repeated-measures ANOVA (attended orientation × perceived orientation) on
225 the Mahalanobis distance, separately for each session and each region. During the preparatory period in the
226 No-Ping session, no significant interaction effects were observed across regions (*ps* > 0.443; Fig 3B). In
227 contrast, the same analyses applied to the Ping session revealed significant interaction effects in visual areas
228 (V1: $F(1,19) = 9.335$, $p = 0.007$, $\eta_p^2 = 0.329$; EVC: $F(1,19) = 8.563$, $p = 0.009$, $\eta_p^2 = 0.311$; Fig 3C; also see
229 Supplementary Table 1), but not for frontoparietal regions (*ps* > 0.213). This cross-region difference is
230 consistent with the function of sensory areas in encoding precise neural representations for basic visual
231 features. To directly compare whether the attentional modulation on Mahalanobis distance was statistically
232 different with and without the visual impulse, we used a three-way mixed ANOVA (session × attended
233 orientation × perceived orientation). The analysis revealed no main effects (*ps* > 0.300 across comparisons)
234 but a significant three-way interaction in V1 ($F(1,38) = 5.00$, $p = 0.031$, $\eta_p^2 = 0.116$; see Supplementary
235 Information, Table 1), suggesting that by "pinging" the brain, the attentional template during preparation
236 became more similar to the perception of corresponding orientation. We also calculated the Mahalanobis
237 distance between neural patterns evoked by the superimposed gratings during the stimulus selection period
238 and each condition in the perception task, finding similar results (see Supplementary Information and S4

Fig). This result was expected, as feature-based attention is known to selectively enhance the representation of task-relevant features while filtering out task-irrelevant ones.

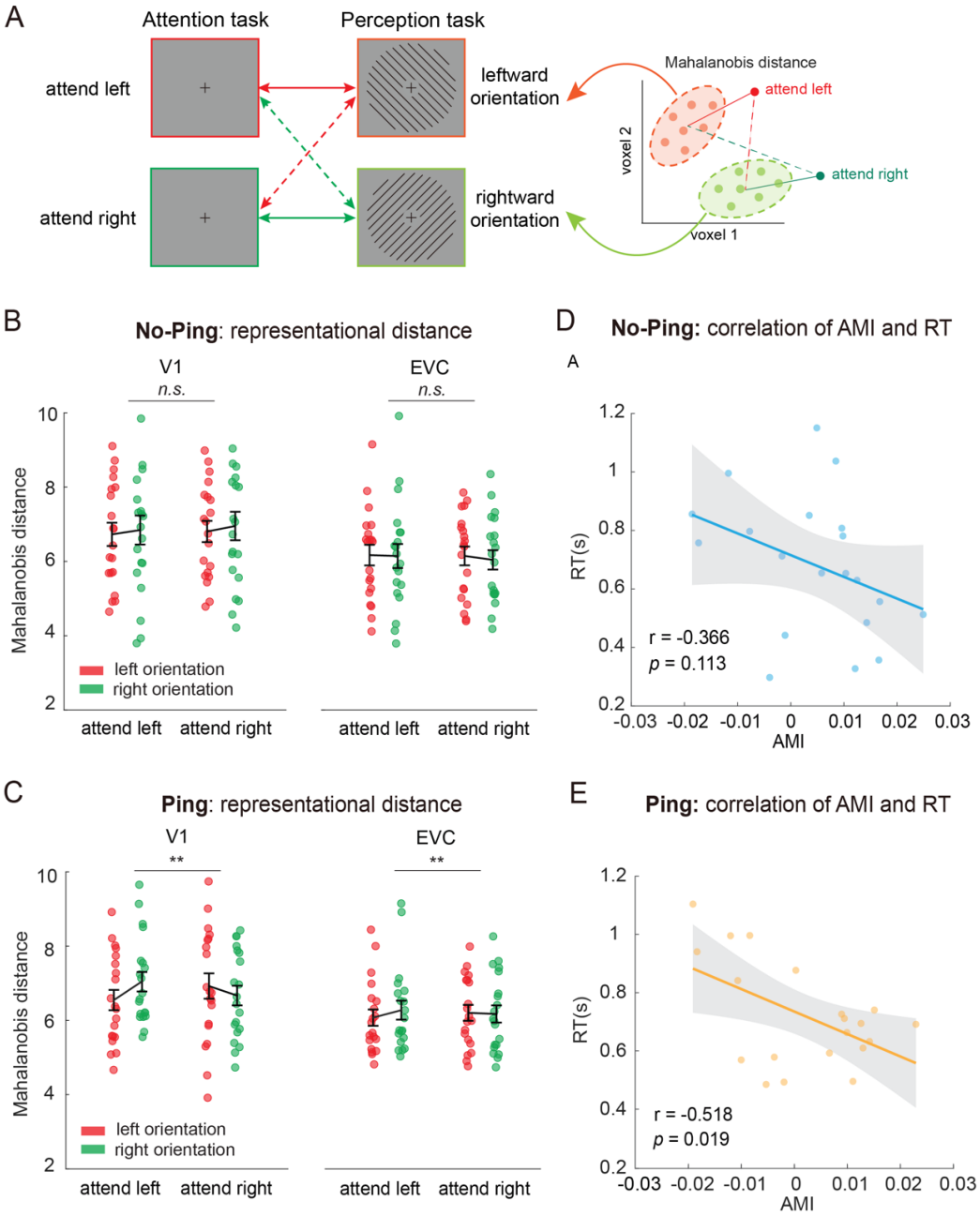

Fig 3. Orientation-selective attentional modulations on neural pattern distances during preparation. (A) Schematic illustration of the representational distance (mean Mahalanobis distances) between each of the attention conditions and each of the perception conditions. Colored arrows indicate measures of the pair-wise Mahalanobis distance. The right panel shows two attention trials (red indicates attend-to-leftward and green indicates attend-to-

246 rightward) to the distribution of each perception condition (shown in a cloud of light-colored dots). (B) Mahalanobis
247 distance between preparatory attention condition and perceived orientation condition in the No-Ping and (C) Ping
248 sessions. Error bars denote SEM. (D) Correlations between attentional modulation index (AMI) and reaction time (RT)
249 in the No-Ping and (E) Ping sessions. Each dot represents one subject's data. The shaded area represents the confidence
250 intervals of the regressed lines. * $p < 0.05$, ** $p < 0.01$.
251

252 The continuous nature of the Mahalanobis distance also made it possible to further investigate
253 potential neural-behavioral correlations. We examined whether activating a sensory-like template during
254 preparation would benefit subsequent orientation processing. In particular, we calculated attentional
255 modulation indices (AMIs) based on trialwise Mahalanobis distance in V1. The index was calculated as
256 follows: AMI = $(D_{different} - D_{same})/(D_{different} + D_{same})$, where D_{same} and $D_{different}$ are the measured distance (D)
257 in the Same (e.g., attend and perceive the same orientation) and Different (e.g., attend and perceive different
258 orientations) orientation condition, respectively (see Methods and Materials). Then, we calculated the
259 correlation between AMI and both reaction time (RT) and accuracy across participants, separately for each
260 session. In the No-Ping session, we observed no significant correlation between AMI in V1 and RT (r = -
261 0.366, p = 0.113; Fig. 3D). By contrast, the same analysis in the Ping condition revealed a significantly
262 negative correlation (r = -0.518, p = 0.019; Fig. 3E). These results indicate that the attentional modulations
263 evoked by visual impulse was associated with faster RTs. These effects were not observed for accuracy
264 ($ps > 0.550$). Furthermore, we also performed within-subject analysis by sorting trials as "strong modulation"
265 and "weak modulation" trials based on each individual's AMI values, facilitated RTs were observed in
266 "strong modulation" trials during the Ping session (Supplementary Information and S3 Fig). These results
267 suggest that the impulse-driven sensory-like template in primary visual cortex is functionally relevant to
268 subsequent attentional selection, providing evidence for the prospective use of sensory-like template in this
269 task. In addition, we did not observe such behavioral differences in analogous analyses using data from the
270 stimulus selection period in either session ($ps > 0.230$), which might due to the potential dilution by strong
271 stimulus-evoked responses during the stimulus selection period.

272 **Activating sensory-like template strengthens the informational connectivity between sensory**
273 **and frontoparietal areas**

274 Selective attention is generally believed to rely on coordinated network activity (Corbetta & Shulman,
275 2002). In particular, studies have shown that functional connectivity between sensory and frontoparietal
276 areas was modulated by attentional control (Bressler et al., 2008; Rosenberg et al., 2020). Given that the
277 impulse-driven sensory-like template facilitated behavior, we reasoned that it may also enhance network
278 communication. Thus, we examined informational connectivity measures to explore how the impulse
279 altered network function during the attention task.

280 We used a method that allows inference based on multivoxel pattern information rather than
281 univariate BOLD response (Jia et al., 2020; Ng et al., 2021). For each ROI, we calculated the cross-validated
282 Mahalanobis distance from each attention trial (from one left-out run) to the distribution of each attended
283 orientation (all trials from remaining runs) during preparation (see Methods and Materials). To quantify the
284 degree of attentional modulation during preparation, we calculated the AMI based on trial-wise
285 Mahalanobis distance and generated a time course of AMI values across trials. Pearson correlation was
286 used to estimate the covariation between each pair of ROIs, the resulting correlation coefficients were
287 transformed using Fisher's z-transform for statistical inference (Fig 4A). The analysis revealed numerically
288 higher levels of connectivity in Ping than in No-Ping session, this impulse-driven increase in connectivity
289 reached statistical significance in two pairs (Fig 4B): V1-IPS (independent t-test: $t(38) = 2.566$, $p = 0.014$;
290 Cohen's d = 0.812) and V1-PFC (independent t-tests: $t(38) = 3.158$, $p = 0.003$; Cohen's d = 0.999). The
291 enhanced functional connectivity between V1 and frontoparietal areas driven by the impulse may
292 potentially facilitate information flow among areas to improve attentional control, as implicated by a trend
293 of ping-enhanced correlations between V1-PFC and RTs (Supplementary Information and S5 Fig).
294 Additionally, the same analysis of AMI based on cross-validated Mahalanobis distance during the stimulus
295 selection period showed no significant differences in information connectivity between No-Ping and Ping
296 sessions (*ps* > 0.224; Supplementary Information and S6A Fig). The lack of changes in long-range

connectivity during stimulus selection period may be attributed to a general rise in connectivity caused by strong sensory inputs in this period, which could have attenuated any potential impacts of visual impulses. Furthermore, connectivity analysis based on mean BOLD response over time did not reveal any significant changes in inter-cortical connections between the two sessions (*ps* > 0.136; S6B Fig), suggesting that the impulse-driven increased information connectivity between V1 and higher-order areas was unlikely contributed by the overall changes of BOLD response.

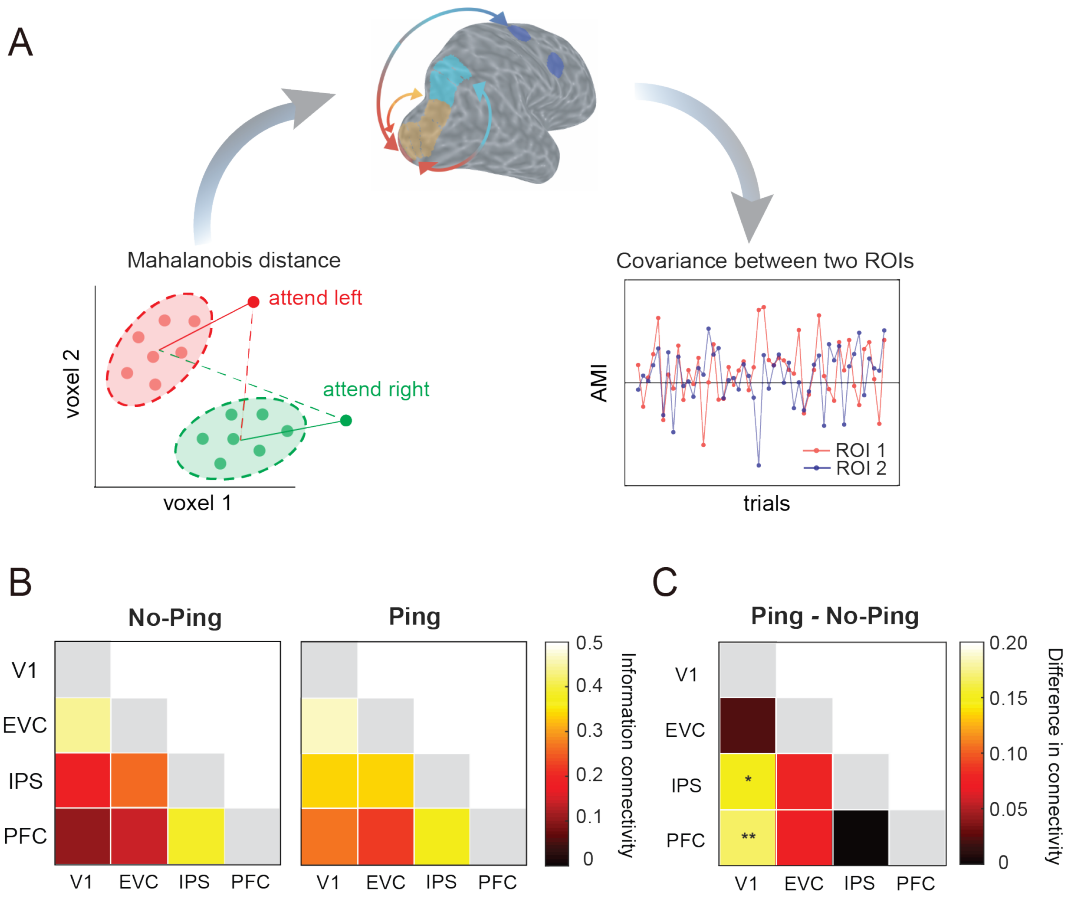

Fig 4. Information connectivity analysis. (A) Schematic illustration of the procedure for the information connectivity analysis in the space of two hypothetical voxels. For each region, we calculated the Mahalanobis distance of the attention trial (from one left-out run) from two attention distributions (all trials from remaining runs). Red and green dots indicate activity patterns from two trials (right panel). The brain image shows an example pair of intercortical information connectivity between V1 and PFC. The time series (lower-left panel) consisted of attentional modulation

index (AMI) based on the Mahalanobis distance. (B) Between-region information connectivity in the No-Ping and Ping sessions. (C) The differences in connectivity between the Ping and No-Ping sessions. * $p < 0.05$, ** $p < 0.01$.

Discussion

While there is ample evidence that the brain can maintain an attentional template of an upcoming target before sensory information is presented (Desimone & Duncan, 1995; Kastner et al., 1999; Summerfield & De Lange, 2014), its representational format remains unclear. To address this, we used an orientation cueing paradigm with separated preparation and stimulus selection periods and applied MVPA to decode neural activity patterns associated with feature-specific attentional information of the upcoming target. The analyses showed robust attentional information both before and after the presentation of the compound grating, indicating a sustained maintenance of attentional templates throughout a trial. Importantly, while the decoders trained on the perception of single orientations could not generalize to preparation until the stimulus selection period (*No-Ping session*), perturbing the brain with a visual impulse resulted in generalizable activity patterns during preparation in V1 and EVC (*Ping session*). These results suggest a predominantly non-sensory format of representation, with a sensory-like template in a latent state during feature-based preparation in the visual cortices. Furthermore, impulse-driven sensory-like template was accompanied by enhanced information connectivity between V1 and frontoparietal areas, as well as enhanced orientation-specific neural modulations of neural distances in the visual areas that predicted levels of behavioral performance. We observed similar response profiles in V1 and EVC, with V1 exhibiting more robust ping-evoked changes compared to EVC, consistent with its primary role in orientation processing (Priebe, 2016). The differences between the Ping and No-Ping sessions could not be attributed to differences in sensory information from the perception task, overall strength of preparatory attention, or differences in eye position (S7 Fig). Therefore, our findings suggest a dual-format neural representation scheme (non-sensory vs. sensory-like) operating in different functional states (active vs. latent). This mechanism may give rise to flexible attentional control, allowing effective transition from coarse to fine attentional templates at various processing stages (initial guidance vs. precise stimulus discrimination).

335 Recent advances in theories of visual search differentiated between the "guiding template" and
336 "target template" based on measures of behavioral performance and eye movements (Wolfe, 2021; Yu et
337 al., 2023). According to these theories, early attentional guidance typically depends on a non-veridical
338 codes that represent only the most diagnostic information, whereas later, target-match processes utilize
339 more precise codes to optimize decision accuracy (Kerzel, 2019; Scolari et al., 2012; Yu et al., 2022). Our
340 study reveals a parallel coding mechanism in the context of feature-based attention, expanding upon these
341 theoretical notions in three key aspects.

342 First, we provide neural evidence for a default, predominantly non-sensory template during
343 preparation, indicating that the concept of a "guiding template", as proposed by visual search theories
344 (Wolfe, 2021; Yu et al., 2023), also applies to preparatory attention in a non-search context. This highlights
345 a shared functional role of a non-veridical attentional template in early guidance across different scenarios.
346 Second, despite the theoretical notion that the brain maintains a more veridical template with detailed target
347 information than is typically utilized to form the guiding template (Wolfe, 2021; Yu et al., 2023), neural
348 evidence supporting this hypothesis is currently lacking. We provide evidence for this notion and propose
349 a plausible neural implementation for preserving a more veridical, sensory-like template in the latent state.
350 A natural question is why the sensory-like template remains latent during preparation. We note that our task
351 requires both coarse and fine featural information. During preparation, a coarse, non-veridical guiding
352 template suffices for target-distractor discrimination, while during stimulus selection, a precise template is
353 needed for the fine discrimination task (reporting the tilted direction of a small angular offset). Maintaining
354 a latent sensory-like template during preparation is thus efficient, as it facilitates future sensory processing
355 while conserving resources. Finally, information connectivity between visual and higher-order
356 frontoparietal regions was enhanced by visual impulse during preparation, which correlated with improved
357 behavioral performance in feature selection. This result suggests that improved information flow across the
358 relevant areas leads to enhanced attentional control, which in turn contributes to refined sensory
359 representations of target in early visual cortex, facilitating transitions from a non-sensory to sensory-like
360 template. Future studies may adopt layer-specific fMRI to infer the direction of this improved information

flow (Jia et al., 2023; Jia et al., 2024) and explore the relationship between long-range connections and the utilization of different formats of target templates.

It could be argued that preparatory attention relies on the same mechanisms as working memory maintenance. While these functions are intuitively similar and likely overlap, there is also evidence indicating that they can be dissociated (Battistoni et al., 2017). In particular, we note that in our task, attention is guided by symbolic cues (color-orientation associations), while working memory tasks typically present the actual visual stimulus as the memorandum. A central finding in working memory studies is that neural signals during WM maintenance are sensory in nature, as demonstrated by generalizable neural activity patterns from stimulus encoding to maintenance in visual cortex (Harrison & Tong, 2009; Serences et al., 2009; Rademaker et al., 2019). However, in our task, neural signals during preparation were non-sensory, as demonstrated by a lack of such generalization in the No-Ping condition (see also Gong et al., 2022). We believe that the differences in cue format and task demand in these studies may account for such differences. In addition to the difference in the sensory nature of the preparatory versus delay-period activity, our ping-related results also exhibited divergence from working memory studies (Wolff et al., 2015, 2017). While these studies used the visual impulse to differentiate active and latent representations of *different items* (e.g., attended vs. unattended memory item), our study demonstrated the active and latent representations of *a single item in different formats* (i.e., non-sensory vs. sensory-like). Moreover, unlike our study, the impulse did not evoke sensory-like neural patterns during memory retention (Wolff et al., 2017). These observations suggest that the cognitive and neural processes underlying preparatory attention and working memory maintenance could very well diverge. Future studies are necessary to delineate the relationship between these functions both at the behavioral and neural level.

While we found that the ping allowed us to detect a sensory-like template during preparation, the underlying neural mechanism of such effects remains unclear. One possibility, as informed by theoretical studies of working memory, is that the sensory-like template could be maintained via an “activity-silent” mechanism through short-term changes in synaptic weights (Mongillo et al., 2008). In this framework, a visual impulse may function as nonspecific inputs that momentarily convert latent traces into detectable

activity patterns (Rademaker & Serences, 2017). Related to our findings, it is unlikely that the orientation-specific templates observed during the Ping session emerged *de novo* from purely non-sensory representations and were entirely induced by an exogenous ping, which was devoid of any orientation signal. Instead, the more parsimonious explanation is that visual impulse reactivated pre-existing latent sensory signals, consistent with the models of "activity-silent" working memory. However, the detailed circuit-level mechanism of such reactivation is still unclear, as well as whether this effect is modality-specific. Prior work shows that only visual, but not auditory, impulses reactivate latent visual working memory (Wolff et al., 2020), suggesting some degree of modality-specificity. However, this finding warrants direct investigation in future studies. Furthermore, we acknowledge that whether pinging identifies an activity-silent mechanism is currently debated (Barbosa et al., 2021; Schneegans & Bays, 2017). An alternative possibility is that the visual impulse amplified a subtle but active representation of the sensory template during preparation. Distinguishing between these alternatives likely requires future studies with more detailed neurophysiological measurements. Regardless of the precise neural mechanism for the observed latent, sensory representation, our results suggest that both sensory and non-sensory templates likely co-exist.

The non-generalizable activity patterns from perception to preparatory attention, in the absence of visual impulse, suggests a default, predominantly non-sensory template during preparation. This finding is largely consistent with electrophysiological studies (Myers et al., 2015; Wen et al., 2019) and our prior fMRI work on preparatory attention to motion directions (Gong et al., 2022), but differs from some previous neuroimaging studies that demonstrated sensory-like templates during preparation (Kok et al., 2014; Peelen & Kastner, 2011; Stokes et al., 2009). One potential account for these discrepancies is that those studies used cue-only trials where the target was expected but not actually presented, in contrast to our task where the target was shown on every trial with temporally separated preparation and stimulus selection periods. This seemingly subtle difference may significantly impact the formats of the neural representations. Because cue-only trials increased the likelihood of target appearance at the subsequent time point, sensory template may be activated due to modulations of temporal expectations (Grubert & Eimer, 2018). This

explanation is consistent with theories suggesting differential influences of expectation and attention on neural activity: expectation reflects visual interpretations of stimuli due to sensory uncertainty, whereas attention is guided based on the task relevance of sensory information (Rungratsameetaweemana & Serences, 2019; Summerfield & Egner, 2009, 2016). Our finding of a predominantly non-sensory format may indicate an optimized coding strategy employed by the brain to effectively and robustly represent information for future use. This aligns with the proposed role of attention in modulating sensory representations to encode only currently relevant information at a minimal cost (Yu et al., 2023).

While our findings cannot pinpoint the exact format of this non-sensory template, we consider categorical coding a plausible candidate based on previous findings. For instance, visual search studies demonstrate that categorical attributes (e.g., steep vs. shallow; left-tilted vs. right-tilted) efficiently guide attention for simple features, such as an orientation or a color (Kong et al., 2017; Wolfe et al., 1992), particularly when features are consistent and predictable (Hout et al., 2017). In our task, the angular relations between the target and distractor orientation were defined by categorical attributes (e.g., left-tilted vs. right-tilted) and remained consistent across trials, making a categorical template feasible during preparatory attention. Furthermore, categorical template allows for greater tolerance of stimulus variability, which is also useful given the trial-by-trial variations in target orientation around the reference orientation in our task. Future studies are needed to address the nature of the non-sensory template during preparation as well as task parameters that might modulate them.

In summary, the current study suggests that there are two formats of attentional templates each having a distinct functional state: a default, non-sensory format and a latent, sensory-like format. This dual-format representation aligns with theories on the dual-function of attentional template for different task goals (Hout & Goldinger, 2015; Yu et al., 2023). The current findings provide a plausible neural implementation for these theories by demonstrating different formats in different functional states. This mechanism likely reflects an optimized coding scheme that effectively balances processing efforts and demands, particularly well-suited for flexible control and transitions from coarse to fine task demands in visually guided behavior.

Materials and Methods

Participants

Twenty individuals participated in the No-Ping session (11 females, mean age = 22.9) and twenty individuals participated in the Ping session (14 females, mean age = 23.7). Among them, 14 participants took part in both sessions, while 12 of them took part in only one session. The sample size was comparable to previous studies using similar attention tasks (Baldauf & Desimone, 2014; Gong & Liu, 2020a; 2020b; Guo et al., 2012; Jigo et al., 2018; Liu & Hou, 2013). Because our primary interest is the generalization from the perception task to attention task, we used the minimal effect size of decoding accuracy across regions (one-sample t-tests: $d = 0.868$) from our previous study with a similar design (Gong et al., 2022), and used G*Power (Version 3.1) (Faul et al., 2007) to confirm that this sample size is sufficient to detect a cross-task generalization effect with a power greater than 95% (a = 0.05). All participants were right-handed and had a normal or corrected-to-normal vision. Participants provided written informed consent according to the study protocol approved by the Institutional Review Board at Zhejiang University (2020-06-001). They were paid ¥200 (~$27.4) for their participation in each session.

Stimuli and Apparatus

Stimuli were generated using Psychtoolbox (Brainard, 1997; Kleiner et al., 2007) implemented in MATLAB. The stimuli were presented on an LCD monitor (resolution: 1920 × 1080, refresh rate: 60 Hz) during behavioral training, at a viewing distance of 90 cm in a dark room. During the fMRI scans, stimuli were projected to a screen via a MR-compatible LCD projector (PT-011, Jiexin Technology Co., Ltd., Shenzhen, China) with the same resolution and refresh rate as the LCD monitor during behavioral training. Participants viewed the screen via an angled mirror attached to the head coil at a viewing distance of 115 cm. Angular stimulus size was the same across behavioral and fMRI sessions.

The orientation stimuli were square-wave gratings (1.3 cycles per deg, duty cycle: 10%) in a circular aperture (inner radius: 1.5°; outer radius: 6°). The gratings flashed on a gray background at 10 Hz, alternating between black and white. There were two types of stimuli: two overlapping gratings orientated

464 leftward (~135°) and rightward (~45°), or a single grating with one of the two orientations (~135° or ~45°).
465 Here, we refer to the 45° and 135° orientations as the reference orientations. The impulse stimulus was a
466 high-contrast, white (at the maximum projector output level) circular disk that covered the same area as the
467 orientation stimulus (radius: 6°).

468 **Experimental Procedures and Tasks**

469 Each participant completed at least two fMRI sessions on different days. One session was used for defining
470 ROIs (see Definition of Regions of Interests), while the remaining sessions were used for the main
471 experiment (see Attention task and Perception task). Before the scanning sessions, participants were trained
472 to familiarize with the tasks in a separate behavioral session. The procedures and tasks were similar to our
473 previous work (Jigo et al., 2018; Gong et al., 2022).

474 *Attention task.* We used a cueing paradigm (Fig 1A). Each trial began with a color cue (red or green)
475 for 0.5 s to indicate the reference orientation of the upcoming target (leftward vs. rightward orientation). In
476 the No-Ping session, the cue was followed by a blank display during the preparation period; in the Ping
477 session, a task-irrelevant, high-luminance visual impulse ("ping", 0.1 s) occurred at either 0.5 s (for short
478 delays of 1.5 s and 3.5 s) or 2.5 s (for long delays of 5.5 s and 7.5 s) after the onset of the cue display. The
479 orders of these sessions were counterbalanced across participants who completed both. Following the
480 preparatory period, two superimposed gratings were then shown for 1 s. The target grating was shown with
481 a small angular offset with respect to the cued reference orientation, whereas the distractor grating was
482 shown in the uncued reference orientation (e.g., if rightward orientation was cued, the rightward grating
483 was shown in 45°± d and the leftward grating was shown in 135°). Note that the angular offset was
484 determined individually based on the threshold obtained during the training session (at least 3 blocks, 30
485 trials/block), using a staircase procedure (Best Parameter Estimation by Sequential Testing, Best PEST), as
486 implemented in the Palamedes Toolbox (Prins & Kingdom, 2009). Participants used a keypad to report
487 whether the attended orientation was more leftward or rightward relative to the reference orientation. Each
488 trial was separated by an inter-trial interval of 3 s to 7 s (2 s per step). Trial-by-trial feedback ("correct" or
489 "incorrect") was provided in the training session but not during scanning. Instead, the percentage of correct

490 responses was provided at the end of each run in the scanning session to avoid the impact of trial-level
491 feedback on neural activity.

492 Given the need to maximize the number of trials for fMRI-based MVPA, we could not accomodate
493 additional conditions (e.g., neutral cue) to measure the behavioral effects of attention. However, our prior
494 work using similar feature cueing paradigms (Liu et al., 2007; Jigo et al., 2018) found that attentional cueing
495 improved behavioral performance relative to a neutral condition. Thus, it is highly likely that our well-
496 trained participants used the cue to direct their attention in the fMRI experiment. Furthermore, our neural
497 measures of attentional signals revealed feature-specific attentional modulations, further validating our
498 approach. To prevent the cue-related sensory difference from contributing to neural activity, we reversed
499 the mapping between colors and orientations halfway through the experiment (e.g., red indicated "attend
500 leftward orientation" and green indicated "attend rightward orientation" in the first half of the runs, and
501 vice versa for the second half of the runs), with the order counterbalanced across subjects. The mapping of
502 colors and orientations was reversed only once in the middle of the experiment to prevent misremembering
503 of the color-orientation associations. To reduce temporal expectancy over a fixed period, the preparatory
504 period (i.e., cue-to-stimulus interval) varied from 1.5 s to 7.5 s with different probabilities (10% for 1.5 s
505 or 3.5 s each, 40% for 5.5 s or 7.5 s each). The long-delay trials (5.5 s or 7.5 s) were selected for subsequent
506 analyses, as they allow the separation of the preparatory activity from the grating-evoked response during
507 fMRI scanning. The short-delay trials were included to encourage a sustained maintenance of attention
508 throughout the entire preparation period.

509 *Perception task.* On each trial of the perception task (Fig 1B), a single grating was shown for 1 s,
510 followed by an inter-trial interval between 3 s to 7 s. To equate the sensory inputs between attention and
511 perception tasks, the orientation was shifted away from the reference orientation by the same angular offset
512 as that used in the attention task with each individual participant's own threshold. Participants performed
513 the same orientation discrimination task by comparing the single orientation to the reference orientation.
514 We provided the percentage of correct responses at the end of each run as feedback.

515 **Eye Tracking and Analysis**

To evaluate the stability of visual fixation, we used Eyelink Portable Duo system (SR Research, Ontario, Canada) to monitor each observer's eye position during the training session at a sampling rate of 500 Hz. One participant's data was not used due to the unstable recording of the eye. The data were then analyzed using custom Matlab code.

To examine whether participants adopted a space-based strategy during the preparatory period in the attention task, such as directing their gaze leftward in attend leftward trials, and vice versa for the attend rightward trials, we analyzed the participants' eye positions recorded during the training session. Horizontal and vertical eye positions were analyzed separately. Paired t-tests were performed to compare horizontal and vertical eye positions between two attention conditions. A two-way mixed ANOVA (2 sessions × 2 attended orientations) was applied to the horizontal and vertical positions, respectively.

fMRI Data Acquisition

Imaging was performed on a Siemens 3T scanner (MAGNETOM Prisma, Siemens Healthcare, Erlangen, Germany) using a 20-channel coil at Zhejiang University (Hangzhou, China). For each participant, we acquired high-resolution T1-weighted anatomical images (field of view, 240 × 240 mm, 208 sagittal slices; 0.9 mm^3 resolution), T2*-weighted echo-planar functional images consisting of 46 slices (TR, 2 s; TE, 34 ms; flip angle, 50°; matrix size, 80 × 80; in-plane resolution, 3 × 3 mm; slice thickness, 3 mm, interleaved, no gap) and a 2D T1-weighted anatomical image (0.8 × 0.8 × 3 mm) for aligning functional data to high-resolution anatomical data.

fMRI Data Preprocessing

Data analyses were performed using mrTools (Gardner et al., 2018) and custom code in Matlab. For each run, functional data were preprocessed with head motion correction, linear detrending and temporal high pass filtering at 0.01 Hz. Data were converted to percentage signal change by dividing the time course of each voxel by its mean signals in each run. We concatenated the 6 runs of the attention task and the 3 runs of the perception task separately for further analysis. One of the attention runs in one subject was excluded due to low accurate performance (<50%).

Definition of Regions of Interests (ROI)

Visual and parietal ROIs. Following previous work (Jigo et al., 2018; Gong et al., 2020b; Gong et al., 2022), for each observer, we ran a separate retinotopic mapping session to obtain ROIs in occipital and parietal areas. Observers viewed four runs of rotating wedges (i.e., clockwise and counterclockwise) and two runs of rings (i.e., expanding and contracting) to map the polar angle and radial components, respectively (DeYoe et al., 1996; Engel, 1997; Sereno et al., 1995). Borders between areas were defined as the phase reversals in a polar angle map of the visual field. Phase maps were visualized on computationally flattened representations of the cortical surface, which were generated from the high-resolution anatomical image using FreeSurfer (http://surfer.nmr.mgh.harvard.edu) and custom Matlab code.

To help identify the topographic areas in parietal areas, we ran 2 runs of memory-guided saccade task modeled after previous studies (Konen & Kastner, 2008; Schluppeck et al., 2006; Sereno et al., 2001). Observers fixated at the screen center while a peripheral (~10° radius) target dot was flashed for 500 ms. The flashed target was quickly masked by a ring of 100 distractor dots randomly positioned within an annulus (8.5° – 10.5°). The mask remained on screen for 3 s, after which participants were instructed to make a saccade to the memorized target position, then immediately saccade back to the central fixation. The position of the peripheral target shifted around the annulus from trial to trial in either a clockwise or counterclockwise order. Data from the memory-guided saccade task were analyzed using the same phase encoding method as the wedge and ring data. Therefore, the following regions of interest (ROIs) in each hemisphere were identified after the completion of this session: V1, V2, V3, V3A/B, V4, V7/IPS0, IPS1 to IPS4.

Frontal ROIs. Following previous work (Jigo et al., 2018; Gong et al., 2020b; Gong et al., 2022), we used a deconvolution approach by fitting each voxel's time series from the attention task with a general linear model (GLM) to determine the event-related activations in the brain (see Supplementary Materials: Deconvolution). For each voxel, we computed the goodness of fit measure (r^2 value), which indicates the amount of variance explained by the deconvolution model (Gardner et al., 2018). The r^2 value represents the degree to which the voxel's time series is correlated with the task events, regardless of any differential

567 responses among conditions. Based on the task-related activation (as indexed by r^2 value) and anatomical
568 criteria, we defined two frontal areas in each hemisphere that were active during the attention task: one is
569 located superior to the precentral sulcus and near the superior frontal sulcus (FEF) and the other is located
570 towards the inferior precentral sulcus, close to the junction with the inferior frontal sulcus (IFJ).

571 **Groups of Region.** To characterize the patterns of neural response across cortical hierarchy and
572 streamline data presentation, we grouped results from the nine areas into four groups based on functional
573 and anatomical considerations: primary visual cortex (V1); extrastriate visual cortex (EVC), consisting of
574 V2, V3, V3ab and V4; IPS, consisting of IPS0 to IPS4; prefrontal cortex (PFC), consisting of FEF and IFJ.
575 Individual areas within each group exhibited qualitatively similar results.

576 Note that we analyzed V1 separately for two reasons. First, previous studies consistently identify
577 V1 as the main locus of sensory-like templates during feature-specific preparatory attention (Kok et al.,
578 2014; Aitken et al., 2020). Second, V1 shows the strongest orientation selectivity within the visual hierarchy
579 (Priebe, 2016). In contrast, the extrastriate visual cortex (EVC; comprising V2, V2, V3AB and V4)
580 demonstrates broader selectivity for complex features (Grill-Spector & Malach, 2004). Therefore, it would
581 be particularly informative to analyze V1 separately for our orientation-based attention paradigm.

582 **Multivoxel Pattern Analysis (MVPA)**

583 **Decoding of attended orientation.** To test if multivariate patterns of activity represent information
584 of the attended orientation, separate MVPA analyses were applied on the activity patterns for the
585 preparation and stimulus selection periods. Following previous work (Jigo et al., 2018; Gong et al., 2020b;
586 Gong et al., 2022), for this analysis, we extracted fMRI signals from raw time series in the long delay trials
587 with correct behavioral responses (~72 trials per attention condition); short delay trials were excluded as
588 they could not provide enough data points to measure preparatory activity. We then obtained averaged
589 BOLD response in a 2 s window for each voxel and each trial in a given ROI, separately for preparatory
590 activity (4 to 6 s after the onset of the cue) and stimulus-evoked activity (4 to 6 s after the onset of the
591 gratings). The response amplitudes across two attention conditions in each ROI were further z-normalized,
592 separately for the preparation and stimulus-related activity. These normalized single-trial BOLD responses

were used for the MVPA. We trained a classifier using the Fisher linear discriminant (FLD) analysis to discriminate between two attended orientations (leftward vs. rightward) and tested its performance with a leave-one-run-out cross-validation scheme. This process was repeated until each run was tested once and the decoding accuracy (i.e., the proportion of correctly classified trials) was averaged across the cross-validation folds. The statistical significance of decoding accuracy was evaluated by comparing it to the chance level obtained from a permutation test (see Permutation test). To assess if the decoding accuracy differed between No-Ping and Ping experiments, we performed two-way mixed ANOVAs (2 sessions × 4 regions) on the decoding accuracy.

Cross-task generalization from the perception task to attention task. Following previous work (Jigo et al., 2018; Gong et al., 2022), to test whether the neural patterns in the preparatory and stimulus selection periods from the attention task reflected sensory processing of isolated features, we trained an FLD classifier using the normalized BOLD responses from the perception task (4 to 6 s after the trial onset) to discriminate leftward vs. rightward orientation. Then, we tested this classifier on the normalized response from the independent runs of attention task to discriminate between attend leftward vs. attend rightward orientations, separately for preparation and stimulus selection periods. The significance of decoding accuracy was compared to the chance level obtained from a permutation test (see Permutation test). To assess if the generalization performance differed between No-Ping and Ping sessions, we performed two-way mixed ANOVAs (2 sessions × 4 regions) on the decoding accuracy.

Neural distance between attended and perceived orientations. The decoding accuracy from the cross-task generalization test reflects a discretized readout of the pattern similarity between different conditions. However, employing continuous similarity measures, such as Mahalanobis distance (Mahalanobis, 1936), could be more reliable compared to decoding accuracy (Walther et al., 2016). Therefore, we calculated the Mahalanobis distance to quantify the pattern similarity between two attended orientations and two perceived orientations. For each participant and each ROI, we have M points (i.e., M trials for each attended orientation) in the N-dimensional space (N = 100, number of voxels). For each data point in the attended orientation condition, we computed its distance to each of the orientation distributions

619 (from the perception task). Averaged distance values were then calculated for each combination of attended
620 orientation and perceived orientation pairs. A sensory-like hypothesis would predict smaller distance
621 between the distribution of the attended orientation (e.g., attend leftward) and the distribution of
622 corresponding orientation (e.g., perceive leftward) compared to the alternative orientation (e.g., perceive
623 rightward). Two-way repeated-measures ANOVA (2 attended orientations × 2 perceived orientations) was
624 applied on the Mahalanobis distance, separately for each region and each session.

625 **Neural-behavioral relationships.** We tested if the representation format during preparatory
626 attention was associated with subsequent behavior. For each trial, we calculated the Mahalanobis distance
627 between the attention conditions (attend leftward and attend rightward) and the perceived orientations
628 (leftward and rightward orientation). We estimated the attentional modulation index (AMI) based on these
629 distance values. This index measures how much attention modulated the pattern similarity for the Same
630 orientation condition (e.g., attend and perceive the same orientation) relative to the Different orientation
631 condition (e.g., attend and perceive different orientations). The index was calculated as follows: AMI =
632 $(D_{different} - D_{same})/(D_{different} + D_{same})$, where D_{same} and $D_{different}$ are the measured distance (D) in the Same and
633 Different orientation condition, respectively. Next, we tested the behavioral relevance of AMI in two ways:
634 (1) Inter-subject analysis: correlated AMI with RT and accuracy across participants, separately for each
635 session; (2) Within-subject analysis: for each participant, we sorted the single-trial AMI values in
636 descending order and selected top-ranked 25% trials and bottom-ranked 25% trials to represent "strong
637 modulation" and "weak modulation" trials, respectively. We then extracted behavioral responses on these
638 selected trials and calculated RT and accuracy for each trial type. Paired t-tests were used to compare
639 between "strong modulation" and "weak modulation" trials in each session.

640 **Informational connectivity analysis.** We used Informational Connectivity (IC) to examine shared
641 changes in pattern discriminability over time, a method that allows inference based on multivoxel pattern
642 information rather than overall BOLD response (Jia et al., 2020; Ng et al., 2021). To track the flow of
643 multivariate information across time (i.e., across trials), we measured the fluctuations (covariance) in
644 pattern-based discriminability by calculating the Mahalanobis distance of each trial to the two attended

645 orientations, using a leave-one-run-out cross-validation scheme. For each ROI, we calculated the
646 Mahalanobis distance between the pattern of activity for each attention trial from one left-out run and the
647 distribution of each attended orientation of the remaining runs. To quantify the degree of attentional
648 modulation, we calculated the AMI using the same formula as mentioned above, where D_{same} and $D_{different}$
649 are the measured distance (D) in the Same and Different condition. This index measures how much the
650 pattern similarity increased for the same attention condition (e.g., attend leftward to attend leftward) relative
651 to the different attention condition (e.g., attend leftward to attend rightward). A positive AMI indicates
652 relative proximity to the same attention condition, whereas a negative AMI indicates relative proximity to
653 the different attention condition. A time course of AMI values was generated across runs and pairwise
654 correlated between ROIs using Pearson correlation analysis and Fisher z-transformed. Independent t-tests
655 were used to compare the connectivity between No-Ping and Ping sessions. To assess the relationship
656 between ICs and behavior, we correlated ICs with RT and accuracy across participants, separately for each
657 session.

658 **Permutation test to evaluate classifier performance**

659 Following previous work (Jigo et al., 2018; Gong et al., 2022), for each brain area, we evaluated the
660 statistical significance of the observed decoding accuracy using a permutation test scheme. We first shuffled
661 the trial labels in the training data and trained the same FLD classifier on the shuffled data. We then tested
662 the classifier on the (unshuffled) test data to obtain decoding accuracy. For each ROI and each participant,
663 we repeated this procedure 1000 times to compute a null distribution of decoding accuracy. To compute
664 the group-level significance, we averaged the 20 null distributions to obtain a single null distribution of
665 1000 values for each ROI. To determine if the observed decoding accuracy significantly exceeds the chance
666 level, we compared the observed value to the 95 percentiles of this group-level distribution (corresponding
667 to $p = 0.05$). Note that these ROIs were pre-defined with strong priors as their activation in attention tasks
668 has been consistently reported in the literature. Nevertheless, for those analyses where multiple comparisons
669 were performed across regions, we applied a Bonferroni-correction to adjust the *p*-values.

Bayesian analysis

To evaluate the strength of evidence for the null hypothesis, we conducted Bayesian analyses (Wagenmakers, 2007) using standard priors as implemented in JASP Version 0.17.1 (JASP Team, 2023). We performed Bayesian t-tests and computed Bayes factor (BF_{01}) to compare between two attention conditions (attend leftward vs. attend rightward). Additionally, we used Bayesian repeated-measures ANOVA and computed the exclusion Bayes factors (BF_{excl}) to assess the evidence for excluding specific effects across all models. A Bayes factor (BF) greater than 1 provides support for the null hypothesis. Specifically, a BF between 1 and 3 indicates weak evidence, a BF between 3 and 10 indicates moderate evidence, and a BF greater than 10 indicates strong evidence (Van Doorn et al., 2021).

Approach to handle partially overlapped samples

Our study used partially overlapping samples, with 14 out of 20 participants completing both No-Ping and Ping sessions, while the remainder completed one of the two sessions. The most important analyses entailed assessing whether decoding accuracy was above chance, for which we used the permutation-based method (see above) within each session. Thus, these analyses were unaffected by the partially overlapping samples. In a few analyses where we compared across sessions, we used statistical tests treating "session" as a between-subject factor. We believe this is a reasonable approach, as a between-subject test is more conservative than a within-subject test, such that any significant effect emerged should be a genuine effect. To be certain, we also conducted additional analyses with "session" as a within-subject factor on the subset of data from the 14 participants who completed both sessions in a counterbalanced order. The results were highly similar to those reported in the main text.

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Original idea by K.J. and M.G. Experiment programmed by Y.C. Data collected by Y.C. Analysis programmed by Y.C., K.J. and M.G. Manuscript drafted by Y.C., T.L., and M.G. Manuscript edited and revised by T.L., J. T., K.J., and M.G.

Data Availability

All data, analyses, and task codes have been made publicly available via the Open Science Framework at https://osf.io/ghaxv/

Competing interests

The authors declare no competing interests.