Flexible top-down modulation in human ventral temporal cortex

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ARTICLE INFO

ABSTRACT

Visual neuroscientists have long characterized attention as inducing a scaling or additive effect on fixed parametric functions describing neural responses (e.g., contrast response functions). Here, we instead propose that top-down effects are more complex and manifest in ways that depend not only on attention but also other cognitive processes involved in executing a task. To substantiate this theory, we analyze fMRI responses in human ventral temporal cortex (VTC) in a study where stimulus eccentricity and cognitive task are varied. We find that as stimuli are presented farther into the periphery, bottom-up stimulus-driven responses decline but top-down attentional enhancement increases substantially. This disproportionate enhancement of weak responses cannot be easily explained by conventional models of attention. Furthermore, we find that attentional effects depend on the specific cognitive task performed by the subject, indicating the influence of additional cognitive processes other than attention (e.g., decision-making). The effects we observe replicate in an independent experiment from the same study, and also generalize to a separate study involving different stimulus manipulations (contrast and phase coherence). Our results suggest that a quantitative understanding of top-down modulation requires more nuanced characterization of the multiple cognitive factors involved in completing a perceptual task.

1. Introduction

To tackle the immense size and complexity of visual inputs, the brain concentrates limited attentional resources on the most informative aspects of visual inputs. The mechanisms of attentional allocation have been an active research area in past years, because of the pivotal role that attention plays in different sensory processes, such as feature binding (Treisman and Gelade, 1980), object recognition (Walther et al., 2002), and scene understanding (Itti et al., 1998). Neuroscientists are particularly interested in the neural substrates of attention. Converging evidence from primate electrophysiology and human neuroimaging suggests that attention induces enhancement in microscopic neuronal activity (Reynolds et al., 2000) as well as macroscopic cortical responses (Gandhi et al., 1999; Murray and Wojciulik, 2004). Such attention-induced response enhancement is thought to produce more robust sensory representations (Kastner and Ungerleider, 2000; Reynolds and Chelazzi, 2004).

Despite the well-established finding of attentional enhancement of neural responses, the precise quantitative nature of attentional enhancement remains unclear. One conventional approach to studying this issue is to characterize the impact of attention on the shape of contrast response functions (CRFs) (Boynton, 2009; Buracas and Boynton, 2007; Reynolds et al., 2000), that is, functions describing the relationship between input stimulus contrast and output neural response. Under the assumption that neural responses follow a fixed parametric form (such as the commonly used Naka-Rushton function (Albrecht and Hamilton, 1982)), attention is characterized as imposing a scaling or additive effect on either input contrast or output response. As illustrated in Fig. 1, attention could have the effects of amplifying the overall CRF (Fig. 1A), enhancing the input contrast (Fig. 1B), or inducing a baseline shift (Fig. 1C). Though mathematically elegant, this approach cannot fully explain some experimental measurements found in the attention literature (Li et al., 2008; Luck et al., 1997; Murray, 2008; Reynolds et al., 2000), and moreover, it is not clear whether this *fixed-parameter approach* generalizes to stimulus dimensions other than contrast. Thus, it remains an open question whether the approach provides a satisfactory account of attentional effects.

In this paper, we advocate moving beyond the fixed-parameter approach and argue that it is more appropriate to consider attention as a flexible process that depends on the specific stimuli and task demands

Fig. 1. Schematics of conventional models of attention and the flexible-attention framework. The first row depicts contrast response functions under unattended ($resp_{unatt}$) and attended ($resp_{att}$) conditions. Arrows indicate attentional enhancement. The second and third rows depict the amount of attentional enhancement under two different metrics: percent enhancement (Equation (1)) and raw enhancement (Equation (2)), respectively. The *response-gain model* posits that attention imposes a scaling effect (g) on the output, and therefore predicts that percent enhancement is a flat function of contrast. The *contrast-gain model* posits that attention imposes a scaling effect (g) on the input contrast, and predicts that both percent enhancement and raw enhancement are inverted U-shaped functions. The *additive-shift model* posits that attention imposes an additive effect (a) on the output, and predicts that raw enhancement is a flat function of contrast. In contrast to these fixed-parameter approaches, the *flexible-attention framework* allows for the possibility that attentional effects are neither constant in percent enhancement nor constant in raw enhancement. Here we depict one possibility where attention disproportionately enhances low-contrast responses.

faced by the observer. In this *flexible-attention framework*, attentional effects cannot simply be reflected by contrasting two attention states (i.e., 'present', 'absent'), but rather, attentional effects depend on specific properties of the cognitive processes involved in a task (e.g., whether a detection or a discrimination task is being performed). Since cognitive tasks can take on a variety of different forms, the effects of attention on neural responses may manifest in different ways, and a fixed parametric function might not accurately capture attentional effects observed in arbitrary experiments. The idea of flexible attention is based upon two well-established notions. First, attentional effects highly depend on many factors, such as stimulus properties, such as stimulus size or uncertainty (Carrasco, 2011; Herrmann et al., 2010; Ling and Carrasco, 2006; Schwedhelm et al., 2016b). Second, it has been a well-established notion that attention is never isolated and closely interacts with many other cognitive processes, such as reward (Baldassi and Simoncini, 2011), decision-making (Luo and Maunsell, 2015; Rahnev et al., 2011; Smith and Ratcliff, 2009; Smith et al., 2004; Vernet et al., 2019), working memory (Gazzaley and Nobre, 2012), expectation (Summerfield and Egner, 2016; Wyart et al., 2012), task manipulation (Andersen et al., 2011; Hayden and Gallant, 2009), and task difficulty level (Ress et al., 2000). However, most prior studies only examined flexible attentional effects on one specific stimulus dimension or task. Especially in neurophysiological studies, typically neurons in only one brain region are recorded. To test the limitations of the fixed-parameter approach and the generality of flexible attention, we need to quantify attentional effects across different brain regions and under different stimulus and task manipulations. Empirical evidence inspiring the flexible-attention framework comes from a recent study (Kay and Yeatman, 2017) in which we measured cortical responses to different stimulus categories while subjects performed different tasks (henceforth referred to as the category study).

Here, we strengthen support for the flexible-attention framework through a re-examination of experimental measurements from a separate study (Kay et al., 2015). In this study, cortical responses were measured for different stimulus positions while subjects performed different tasks (henceforth referred to as the *position study*). We quantify attentional effects in human ventral temporal cortex (VTC) as a function of stimulus eccentricity, and apply the same type of analysis to the category study, thereby allowing direct comparison of results. Across studies, we show that weak stimulus-driven responses receive disproportionately large attentional enhancements and that attentional enhancements are more pronounced for certain tasks compared to others. Such effects are not easily explained by conventional models of attention, and therefore suggest the need to develop a more flexible framework for attention. As such, the central novelty of the present study is to analyze a large bulk of data across different studies under different stimulus and task manipulations to reveal the generality of flexible attention theory, directly in contrast to most existing studies that merely focus one specific stimulus dimension or task. In the Discussion, we propose specific ways in which the concept of "flexible attention" might be formalized into quantitative models.

2. Materials and methods

Experiment and MRI data acquisition. Three adults participated in the position study (Kay et al., 2015). In the *task experiment* of that study (Fig. 2), face stimuli (3.2° diameter) appeared at different positions of a 5 × 5 spatial grid (1.5° spacing). This grid sampled six distinct eccentricities (0°, 1.5°, 2.1°, 3°, 3.4° and 4.2°). Each trial consisted of 7 sequentially presented faces (500 ms/face) at a single position but with various identities and viewpoints. Some trials involved two consecutive faces
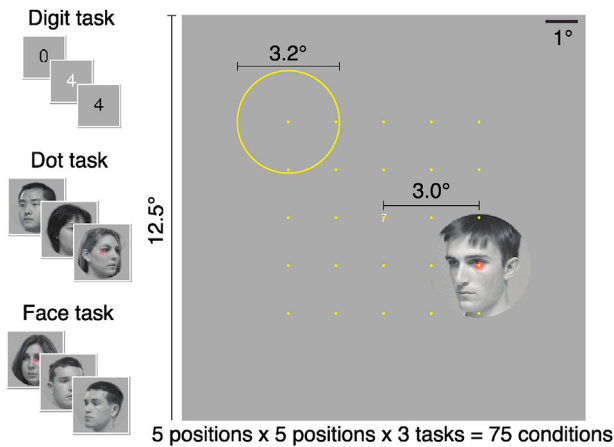
Fig. 2. Stimuli and tasks from the position study (Kay et al. (2015). In a given trial, a sequence of face stimuli (7 face images) appears in one of the twenty-five positions. The *digit task* is a one-back task on the stream of digits at the center-of-gaze. The *dot task* is to detect the occurrence of a red dot on the faces. The *face task* is a one-back task on the identity of the faces. Subjects maintained central fixation, and stimuli were identical across the three tasks.

sharing the same identity but different viewpoints, and some trials involved a red dot appearing at the center of the faces (coincident with one of the 7 faces). A stream of digits ($0.3°$ × $0.3°$) was placed at the center-of-gaze. The identity of the digit (0–9) changed every 0.5 s: each digit was presented for 0.25 s and was followed by a delay of 0.25 s. To minimize visual adaptation, the digit color alternated between black and white on successive presentations. Digit repetitions occurred with a probability of 0.052, with a maximum of two successive identical digits allowed (this matches the overall frequency of digit repetitions to the overall frequency of dot occurrences and the overall frequency of face-identity repetitions). In a given run, participants were instructed to perform either (1) a digit task, during which participants pressed a button whenever the same digit repeated; (2) a dot task, during which participants pressed a button whenever a red dot appeared; or (3) a face task, during which participants pressed a button whenever the same face identity repeated within a trial. Participants fixated the central stream of digits during all three tasks (verified using an eyetracker). There were 75 experimental conditions (25 locations × 3 tasks) and 8 trials for each condition throughout the experiment. All experimental details are described in Kay et al. (2015).

The position study also included another experiment, called the *interleaved-task experiment*. This experiment was the same as the task experiment (Fig. 2) except that the three tasks were randomly intermixed in a trial-by-trial fashion within each run. A central red letter ($0.3°$ × $0.3°$) presented at the beginning of each trial served as a cue for which task to perform. This experiment provides an additional, independent set of data.

Functional MRI data were collected at the Stanford Center for Cognitive and Neurobiological Imaging using a 3T GE Signa MR750 scanner, a Nova 16-channel visual RF coil, and a gradient-echo EPI pulse sequence (TR 2 s, 2-mm voxels). The fMRI data were pre-processed by performing slice time correction, spatial distortion correction, and motion correction. The fMRI data were further analyzed using GLMdenoise (Kay et al., 2013) to estimate the percent blood-oxygenation-level-dependent (BOLD) signal change (beta weight) evoked by each stimulus location under each task. This analysis also generated 100 bootstrap samples of beta weights via resampling of scanning runs.

Visual field maps (V1, V2, V3, and hV4) were defined using standard retinotopic mapping scans. Three face-selective regions (inferior occipital gyrus, IOG-faces/OFA (abbreviated IOG); posterior fusiform gyrus, pFus-faces/FFA-1 (abbreviated pFus); and middle fusiform gyrus, mFus-faces/FFA-2 (abbreviated mFus)) were defined using independent functional localizer scans. We also defined IPS as an additional ROI (beyond

that described the original paper). Specifically, we used the IPS-0 region from an atlas of visual topographic organization (Wang et al., 2015); this choice is reasonable given the limited coverage of parietal cortex available in the position study and the localization of top-down modulation to IPS-0/1 as shown in Kay and Yeatman (2017).

Region-level analysis. After the GLM analysis, we pooled voxels within regions of interests (ROIs) across subjects and hemispheres. The same voxel selection criterion (goodness-of-fit of the population receptive field model) used in our previous paper was applied to exclude non-spatially selective voxels (Kay et al., 2015). To calculate region-level responses, we first computed the median across bootstrap samples to obtain the response of each voxel to the 75 experimental conditions. We noticed that voxels with population receptive fields in the periphery often exhibit negative BOLD responses when face stimuli appear in the central visual field. To avoid this complication, we positively rectified all voxel responses. Note that this should drive our main conclusions as most negative responses appeared in low-level visual cortex such as V1 but the most pronounced attentional effects are found in high-level visual regions (e.g., mFus, Fig. 4). Such negative BOLD responses are unlikely due to attention. Finally, we calculated the region-level response by computing the mean across voxels.

Two metrics were used to quantify the magnitude of attentional effects: *percent enhancement* and *raw enhancement*, which are defined as follows:

$$\text{Percent enhancement} = (R_{\text{dot/face}} - R_{\text{digit}}) / R_{\text{digit}} \times 100, \qquad (1)$$

$$\text{Raw enhancement} = R_{\text{dot/face}} - R_{\text{digit}}, \qquad (2)$$

where $R_{\text{dot/face}}$ indicates an ROI's response for a stimulus location in the dot or the face task and R_{digit} indicates the ROI's response to the same location in the digit task. These calculations provide 50 values (25 for the dot task and 25 for the face task) for each metric.

Analysis of data from the category study. We reanalyzed data from the category study (Kay and Yeatman, 2017) using the same methods described above. In brief, the category study involved presentations of words, faces, and other stimulus categories varying in contrast and phase coherence. Subjects performed one of three tasks: (1) a fixation task, during which participants pressed a button whenever the fixation dot turned red; (2) a categorization task, during which participants reported whether the stimulus was a word, face, or neither; and (3) a one-back task, during which participants pressed a button whenever an image was repeated twice in a row.

In Figs. 6–8, we directly compare results across the position and category studies. To facilitate comparison, we pooled voxels from pFus and mFus in the position study to match the definition of FFA in the category study. In Fig. 7, since overall BOLD response amplitudes might vary for incidental reasons across subjects, we normalized the bottom-up responses (responses during the digit task of the position study and responses during the fixation task of the category study) by dividing by the maximal BOLD response amplitude observed in each study and ROI. For example, the full set of bottom-up responses measured from FFA in the category study (including contrast and phase-coherence manipulations) was divided by the maximum response. Note that this normalization affects raw enhancement values but not percent enhancement values.

Error bars and statistical analyses. Unless otherwise indicated, error bars indicate 68% confidence intervals (corresponding to plus-or-minus one standard deviation of a Gaussian noise distribution), obtained by bootstrapping across locations that share the same eccentricity (position study) or bootstrapping across subjects (category study). In the position study, we regressed every bootstrap sample on stimulus eccentricity (excluding eccentricity 0 given the availability of only one data point) to obtain the slope of attentional effects as a function of eccentricity. We then derived one-tailed significance values based on the bootstrapped slope distribution (Figs. 4,5 and 6A-B). Similarly, we calculated the statistical significance of regression slopes with respect to stimulus contrast and phase coherence in the category study (Fig. 6C–F).
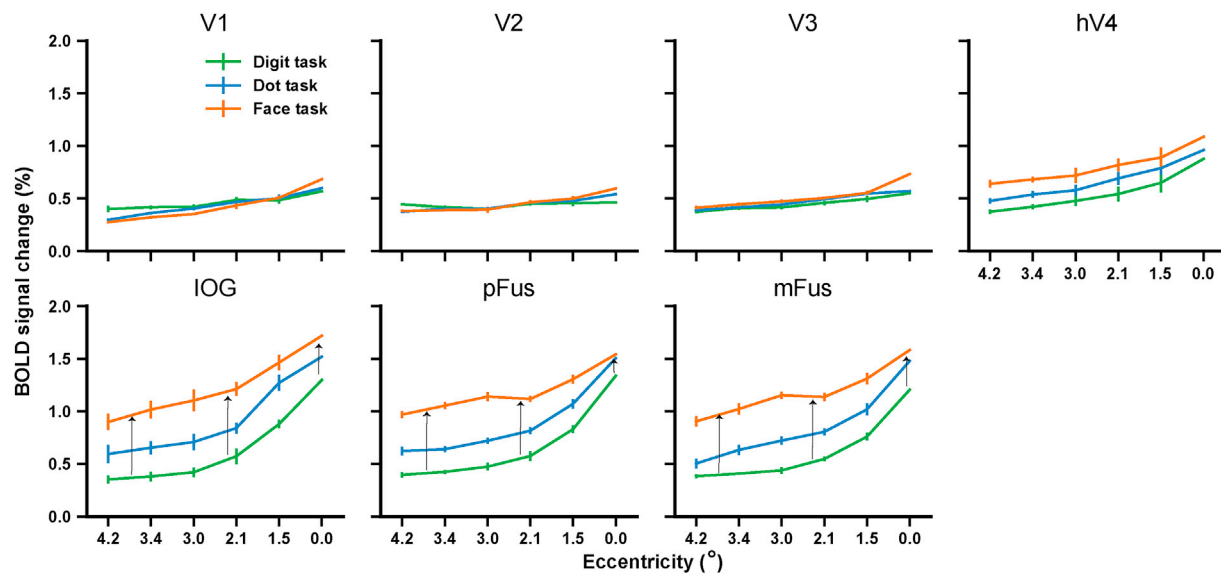
Fig. 3. Percent BOLD signal change as a function of stimulus eccentricity and task. The order of stimulus eccentricity is reversed to make eccentricity-response functions visually comparable to contrast-response functions. BOLD responses are pooled across subjects and hemispheres (see Methods). Error bars indicate 68% confidence intervals on the bootstrapped mean of responses across locations at the same eccentricity (note that 0° corresponds to only one location and thus has no error estimate). Unless specifically mentioned, the same error-bar convention is used in subsequent figures. Responses in high-level visual areas exhibit substantial dependence on both eccentricity and task. Black arrows highlight the disproportionate attentional enhancement at high eccentricities, reminiscent of the schematic of the flexible-attention framework in Fig. 1.
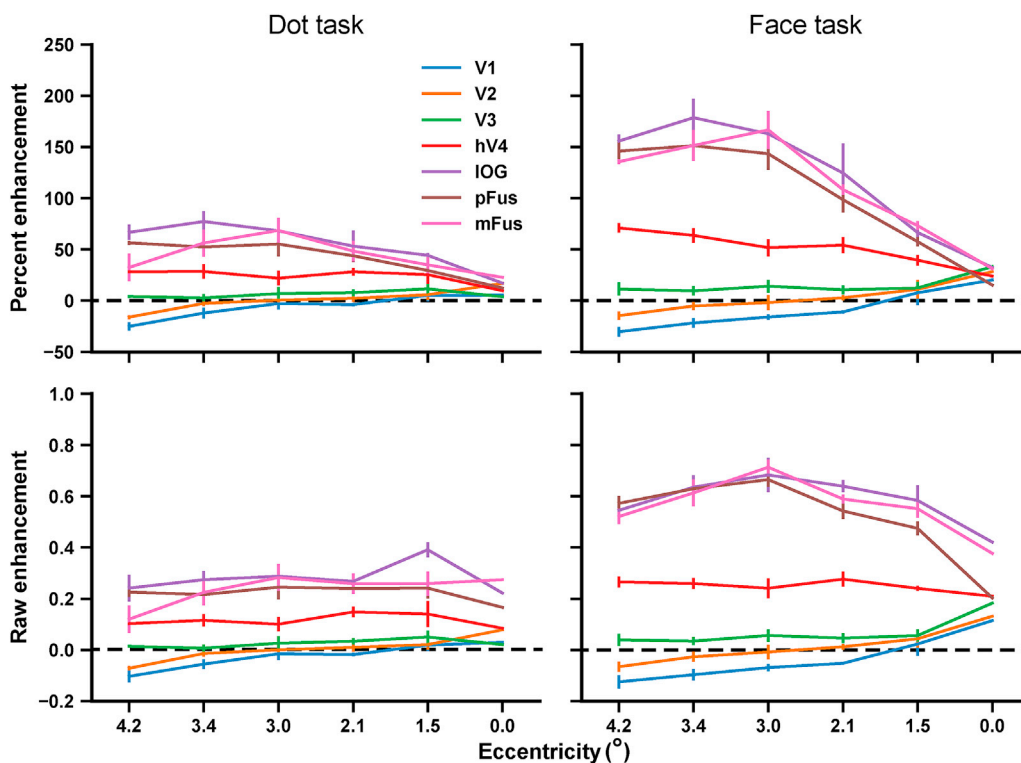
Fig. 4. Attentional enhancement as a function of stimulus eccentricity and task. BOLD responses during the stimulus-relevant tasks (dot and face tasks) are expressed as percent enhancement (upper row) and raw enhancement (bottom row) relative to the responses during the digit task. The horizontal dashed line indicates no attentional enhancement. The magnitude of the attentional effect increases from fovea to periphery, from the dot task to the face task, and from low-level to high-level visual areas. This pattern is inconsistent with the three conventional models of attention (see explanations in the main text). Note that the data point at 0° corresponds to only one location and thus has no error estimate.
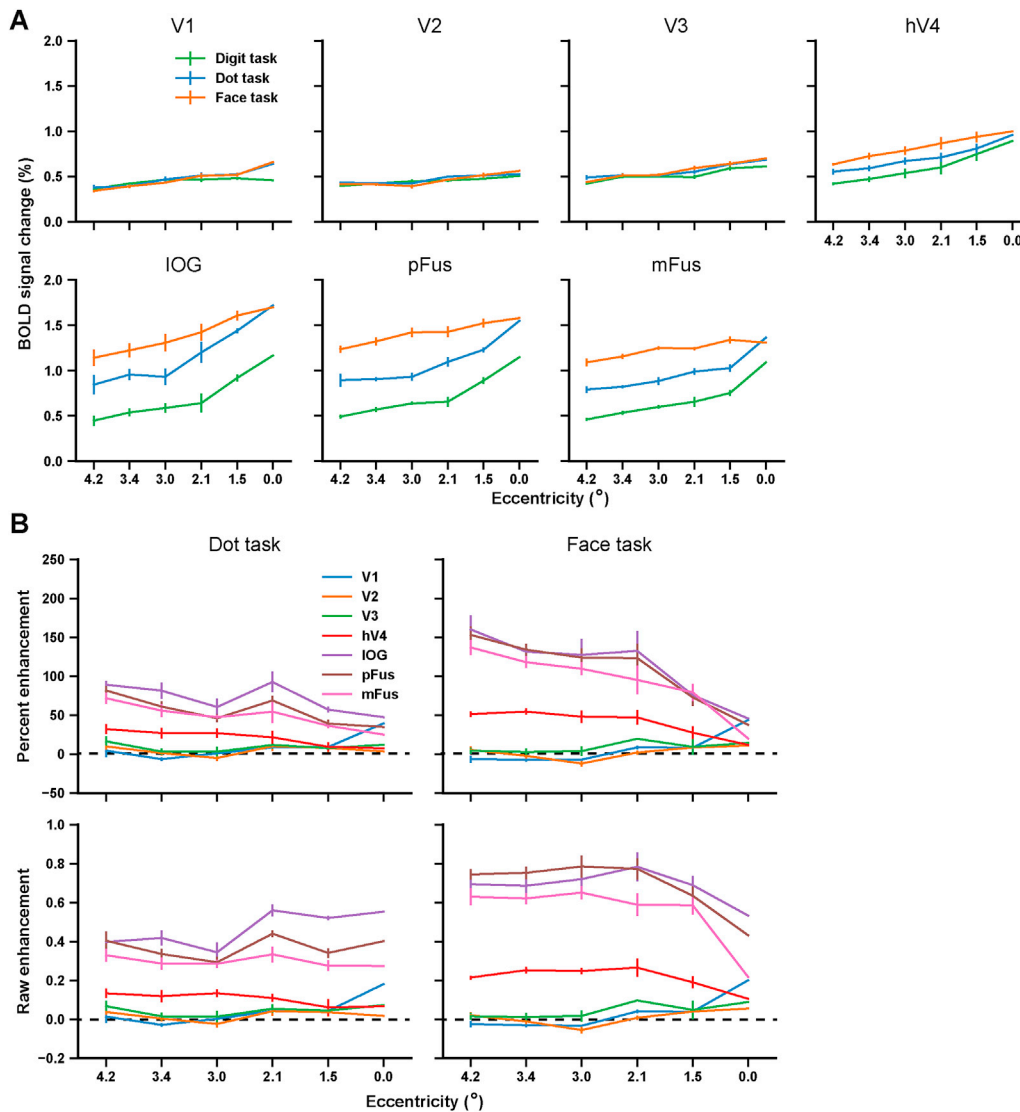
3. Results

3.1. Cortical responses as a function of stimulus eccentricity and behavioral task

We refer to the main experiment in the position study as the *task experiment* (see Methods for details). In the task experiment, participants performed three different cognitive tasks on face stimuli that appeared at

six different eccentricities while BOLD signals in human ventral temporal cortex were measured. Using face stimuli rather than artificial visual stimuli (e.g., checkerboards) produces strong responses not only in early visual areas but also in high-level category-selective regions. This allows us to assess attentional effects throughout the visual cortical hierarchy.

Participants performed three different tasks. The *digit task* is a one-back task on a stream of digits placed at the center-of-gaze. Face stimuli in this task are irrelevant to the participants, and the purpose of this

Fig. 5. Disproportionate attentional enhancements at high eccentricities in the interleaved-task experiment. **A-B**. Results are plotted in the same format as the results from the task experiment shown in Figs. 3–4. Overall, the results from the two independent experiments are highly consistent.

task is to maintain participants' attention at the central fixation point. Although participants may occasionally attend to the face stimuli, we interpret responses in the digit task as primarily reflecting bottom-up visual processing with minimal top-down influences. The *dot task* requires participants to detect the occasional appearance of a red dot superimposed on the face stimuli. In this task, face features (e.g., identity, viewpoint) are irrelevant to the participants. The *face task* requires participants to perform a one-back task on face identity; thus, face features in this task are highly relevant to the participants.

We summarized the responses of each region-of-interest (ROI) as a function of stimulus eccentricity, producing eccentricity-response functions (ERFs). This is analogous to conventional contrast-response functions where responses are plotted as a function of stimulus contrast. Examining the ERFs allows us to inspect whether attentional effects observed for contrast response functions generalize to other feature dimensions. We discovered several prominent effects. First, the evoked responses in high-level face-selective areas generally decrease as stimulus eccentricity increases (Fig. 3), indicating that stimulus eccentricity, like contrast, has a strong influence on cortical responses. Second, the fact that responses increase from the dot task to the face task suggests that the brain enhances responses if the task requires detailed processing of the attended stimulus. Finally, the effect of task on cortical responses

increases along the visual cortical hierarchy, suggesting that attentional effects are more pronounced in brain regions whose representations are critical to the successful execution of the task (i.e., face-selective regions for judging face identity).

3.2. Conventional models of attention cannot fully account for observed attentional effects

We next evaluate the accuracy of different attentional models. We quantified attentional effects as a function of stimulus eccentricity and task using two metrics: *percent enhancement* (Equation (1)) and *raw enhancement* (Equation (2)). These metrics were used because they allow direct assessments of the accuracy of the response-gain and the additive-shift models of attention (Fig. 1). Results indicate that previously proposed models of attention do not fully account for the data (Fig. 4, note that our ROI-averaging approach is different from typical studies of attention—see Discussion). The reasons are as follows.

First, the response-gain model posits that attention amplifies the overall magnitude of ERFs, leading to larger attentional effects when bottom-up stimulus-driven responses are larger, i.e., when the stimulus is in the central visual field. It also predicts percent enhancement will be a flat line as a function of stimulus eccentricity. These predictions are not
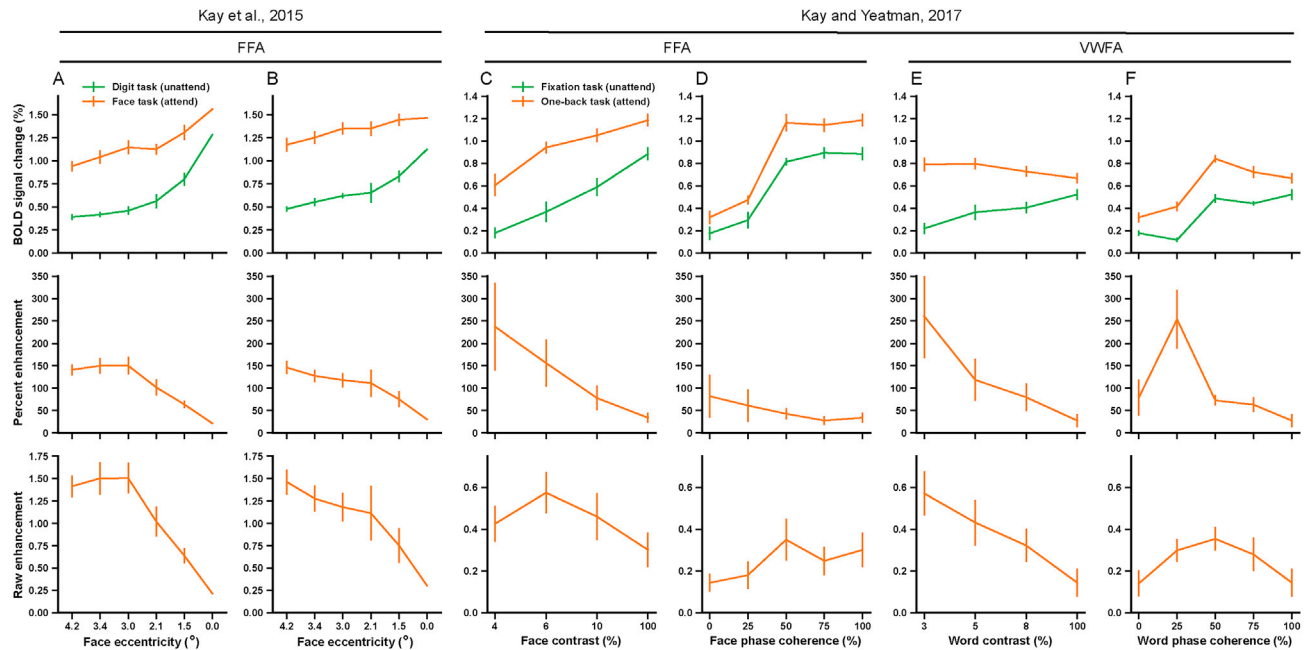
Fig. 6. Disproportionate attentional enhancements generalize across experiments. Panels A–B show results from the position study for the task and the interleaved-task experiments, respectively. Panels C–F show results from the category study. Data from that study have been analyzed in the same way as Panels A–B, except that the error bars reflect 68% confidence intervals on the mean across subjects (see Methods for details). Across metrics, the amount of attentional enhancement generally decreases as stimulus strength (eccentricity, contrast, and phase coherence) increases. Enhancement tends to be greatest when stimulus strength is low and bottom-up responses (green curves in the first row) are weak.

consistent with Fig. 4: raw enhancement is not large in the fovea and there is a clear rising trend of percent enhancement from fovea to periphery in the face-selective regions for both tasks (Fig. 4, bootstrap test, all p-values < 0.05 except for mFus in the dot task where $p = 0.466$).

Second, the additive-shift model posits that attention vertically shifts ERFs; thus, raw enhancement should be a flat function of stimulus eccentricity. This prediction appears consistent with the data in the dot task. The dot task, however, involved no demands for processing face features and the ROIs exhibiting the largest attentional effects are face-selective regions (also see Discussion). In the face task, raw enhancement as a function of eccentricity is not a flat line and instead rises in pFus as stimulus eccentricity increases (Fig. 4, bootstrap test, $p < 0.001$).

Finally, the contrast-gain model predicts the largest percent enhancement and raw enhancement in middle levels of eccentricity, resulting in inverted U-shaped functions of percent enhancement and raw enhancement (Fig. 1B). This model also does not appear to be completely consistent with the data, since the strongest attentional effects, under both metrics, appear in the far visual periphery (also see Discussion).

Since the results are inconsistent with attentional models proposed in previous literature, we propose the idea of flexible attention in which attentional effects do not necessarily conform to simple parametric changes. Before elaborating on this idea, we show first that the observed effects are not idiosyncratic features of this particular experiment but generalize across several stimulus and task manipulations.

3.3. Reproducible effect of flexible attention in an independent dataset

The results reported above are based on data from the task experiment where three different cognitive tasks were performed in different scanning runs. We also conducted an *interleaved-task* experiment in which tasks were interleaved in a trial-by-trial fashion within a run (see Methods for details). This experiment provides an independent dataset that can be used to validate the findings above. We applied the same analysis above on the data from the interleaved-task experiment. The two independent experiments yield highly consistent results (Fig. 5). Percent enhancement increases as stimulus eccentricity increases in all three

face-selective regions in both tasks (bootstrap test, all p-values < 0.05). Raw enhancement also exhibits increases with eccentricity in the face task (bootstrap test, $p < 0.05$ for pFus). Here we used a covert attention paradigm such that some attention is already deployed to the stimulus in fovea. Future studies might consider explicitly manipulate both eye fixation and attention to investigate such fovea bias of attention.

3.4. Evidence for flexible attention in other experimental manipulations

The idea that attentional effects may not be captured by simple parametric forms was motivated by observations in Kay and Yeatman (2017) (termed the *category study*) in which responses to different stimulus categories are measured. In that study, we reported that attention selectively imposes larger scaling effects on weaker responses, a phenomenon termed "stimulus-specific scaling". To consolidate evidence for flexible attention across studies, we apply the same analyses demonstrated above to the data from the category study. The data from that study have two major attractions: (1) In the position study, only one stimulus feature–eccentricity–is manipulated. In the category study, stimuli are manipulated in both contrast and phase coherence, thus providing two extra feature dimensions that influence bottom-up visual processing. (2) In the category study, responses in another ROI–visual word form area (VWFA)–were also measured. This allows us to test whether our findings are specific to FFA or generalize to other high-level visual regions.

We extracted BOLD responses in FFA and VWFA toward their preferred stimulus categories–faces and words, respectively. To make data from the two studies more comparable, voxels from pFus and mFus in the position study were pooled, consistent with the definition of FFA in the category study. Furthermore, we highlight data from the stimulus-relevant tasks that yield the strongest attentional effects: the face task in the position study and the one-back task in the category study.

The two studies show a consistent pattern (Fig. 6): attentional effects are larger for stimuli that evoke weak bottom-up responses (digit task in the position study and fixation task in the category study). In the position study, attentional effects in FFA increase as stimulus eccentricity

increases (Fig. 6A and B, all *p*-values < 0.001). In the category study, we find the same attentional effects with respect to decreasing stimulus contrast in both FFA and VWFA (Fig. 6C, E, all *p*-values < 0.001 for both percent and raw enhancement metrics). As explained previously, neither the response-gain nor the additive-shift model of attention can account for the results. Instead, these results suggest the need for the flexible-attention framework (Fig. 1D). One exception to the general pattern of large attentional enhancement at weak stimulus strength lies at phase coherence data (i.e., Fig. 6D). In Fig. 6D, the percent enhancement increases as phase coherence decreases (*p* < 0.001) but the raw enhancement does not exhibit a clear decreasing pattern (*p* > 0.05). We speculate that this may be because that 0% phase coherence images contain pure noise. A one-back decision task on noise pattern can be very easy and looks qualitatively different from the face and word one-back tasks *per se* (also see Discussion). Nonetheless, this still highlights the need to develop a formal quantitative model to characterize exact demand in a task.

To gain further insight into the relationship between bottom-up responses and the magnitude of attentional enhancement, we plot percent enhancement and raw enhancement values against the bottom-up responses across stimuli, tasks, studies, and ROIs (Fig. 7). The clear inverse relationships between bottom-up responses and the amount of attentional enhancement indicate that attention disproportionately enhances weak neural responses.

3.5. Larger responses in IPS in high-demand tasks compared to low-demand tasks

Why does the brain disproportionately enhance responses to some stimuli and under some tasks compared to other experimental conditions? We suggest that this flexibility in attentional enhancement reflects the interaction between attention and the process of evidence accumulation to accomplish a perceptual decision. In this sense, attention is just one component of a perceptual task and we must consider other top-down processes, such as decision-making, when interpreting the top-down modulation of neural responses. Stimuli with certain properties (e.g., low contrast, low phase-coherence) may yield weak or noisy sensory signals, and may therefore require extra decision time to complete the evidence accumulation process. We have identified the intraparietal sulcus (IPS) as a potential region that is involved in evidence accumulation and that may be the source of top-down enhancement of visually evoked responses (Kay and Yeatman, 2017), which is based upon the rich literature on the link between LIP activity to decision in primates (Roitman and Shadlen, 2002; Shadlen and Newsome, 2001).

Following this approach, we compared IPS responses across the various stimulus manipulations and tasks. IPS exhibited greater activity in the face task compared to the dot task in the position study (Fig. 8A

and B). This is in line with the more pronounced attentional effects observed in VTC for the face task. The result also mirrors the finding of greater IPS activity in the one-back task compared to the categorization task in the category study (Fig. 8C and D). The flexible-attention framework also suggests that IPS activity might depend on the specific stimulus being judged. Indeed, a relationship between IPS activity and contrast and phase-coherence levels was established in Kay and Yeatman (2017). However, in the position study, we did not find a systematic correlation between IPS activity and attentional effects as a function of eccentricity, possibly due to the limited slice coverage and limited statistical power (see Discussion).

4. Discussion

In this article, we analyzed cortical responses in human VTC as a function of stimulus eccentricity and task. We found that the degree of attention-induced response enhancement increases from fovea to periphery and from a face-unrelated task to a face-related task. Moreover, analyses revealed consistent results in an independent experiment in the same study as well as another study involving additional stimulus manipulations and ROIs. Taken together, these results provide new constraints for models of attention and suggest that the effects of attention are dependent on stimuli and tasks in ways that are not captured by simple parametric models of attention that have been previously proposed. Understanding the mechanisms of attention might require further delineating the interaction between attention and other cognitive processes (e.g., decision-making).

4.1. Previous models of attention do not account for the observed effects

Prior research on the quantitative nature of attention has investigated the impact of attention on the shape of CRFs (Boynton, 2009; Li et al., 2008; Murray, 2008). This approach has prompted several influential computational frameworks, such as the response-gain model (McAdams and Maunsell, 1999), the contrast-gain model (Martinez-Trujillo and Treue, 2004; Reynolds et al., 2000), the additive-shift model (Buracas and Boynton, 2007), or the mixture of these models (Huang and Dobkins, 2005; Schwedhelm et al., 2016a). They used the fixed parametric form (i.e., Naka-Rushton function) to summarize the neural consequences induced by attention. One attraction of this fixed-parameter approach is that data from monkey electrophysiological, human fMRI, and psychophysical studies can be analyzed and compared within a common mathematical framework. Boynton (2009) used CRF modeling to summarize findings from seven different studies. Among three fMRI studies in his analysis, results in Buracas and Boynton (2007) and Murray (2008) are better explained by the additive-shift model, while results in Li et al. (2008) are better explained by the contrast-gain model. We acknowledge
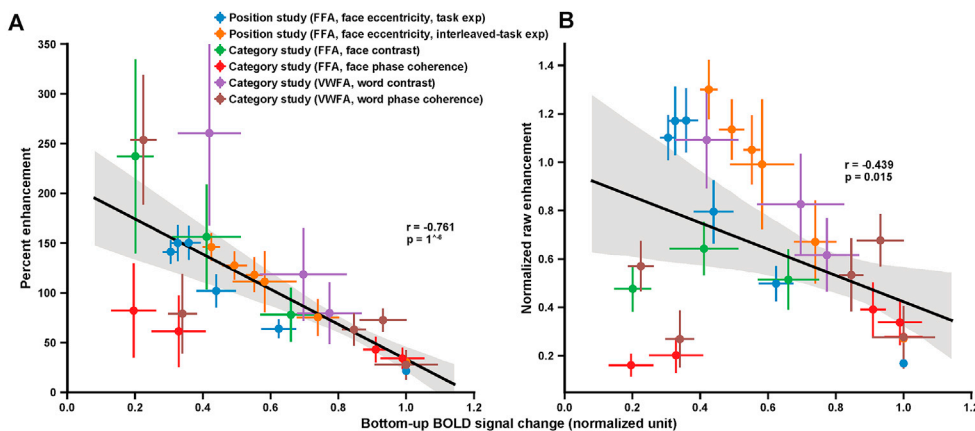
Fig. 7. Inverse relationships between normalized bottom-up responses to percent enhancement (**A**), and normalized raw enhancement (**B**). All data points from the two studies depicted in Fig. 6 are plotted. To ensure that BOLD responses from different ROIs and experiments are in comparable units, we normalize the full set of responses observed during the bottom-up tasks (the digit task in the position study and the fixation task in the category study) in each ROI to a maximum of 1 (see Methods). The shaded area indicates the 95% confidence interval of a bootstrapped best-fit line. The results demonstrate that attentional enhancement tends to be greatest for stimuli that elicit weak bottom-up responses.
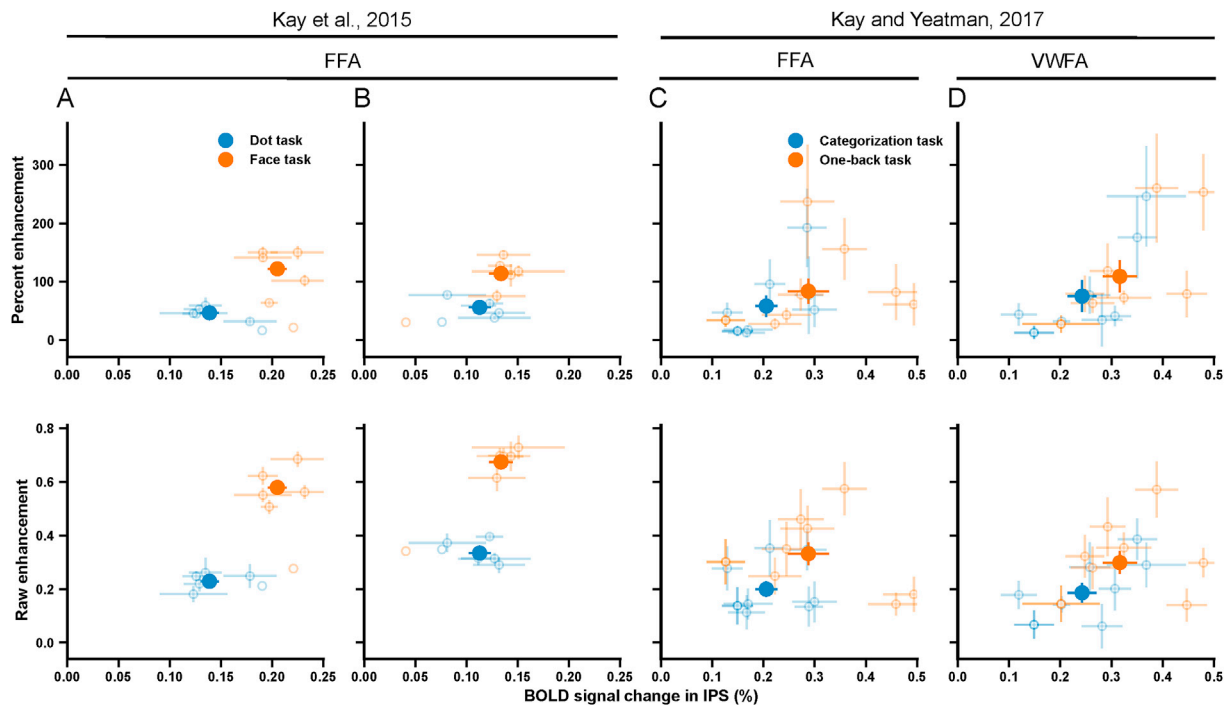
Fig. 8. Percent enhancement and raw enhancement as a function of IPS activity. ***A-B***. Data from the position study (task experiment and interleaved-task experiment, respectively). The small open dots indicate different eccentricities, and the large solid dot indicates the mean across all locations. ***C-D***. Data from the category study. The small open dots indicate individual contrast and phase-coherence levels, and the large solid dot indicates the overall mean. The results show that IPS activity is larger for the face task compared to the dot task and for the one-back task compared to the categorization task, and this is accompanied by larger attentional enhancements in FFA and VWFA.

that the fixed-parameter approach can explain some empirical observations in previous studies. Especially, this approach can well explain results in some electrophysiological experiments. Here we do not completely reject these results; we can only conclude that these models do not provide satisfactory explanations at least for our data (see Results).

With regard to the contrast-gain model, it is theoretically possible that attention shifts contrast response functions so far to the left such that only the upper asymptotic part of the response is observed, and this might be one way of attempting to reconcile the contrast-gain model with our measurements. However, notice that the contrast-gain model predicts that attention should produce no response difference at high contrast (i.e., 100%), but we can still see clear response differences at 100% contrast as well as 100% phase coherence and at the fovea (upper row in Fig. 6). Note that such differences may not be visible in empirical datasets as it relates to the saturation point, the partial data sampling, or measurement noise in CRFs. One recent psychophysical study proposed a new baseline-shift model assuming that attention induces an additive enhancement of input stimulus intensity (Cutrone et al., 2014). This model in theory can produce the CRFs that look like our results here. But this mechanism has been rarely discovered at the neural level.

Another limitation of the CRF modeling approach is that it is essentially a descriptive approach that merely summarizes the apparent structure of data into a function with a few parameters. A Naka-Rushton function may fit any shape of nonlinear CRFs by properly tweaking parameters. A deeper problem is that this approach does not attempt to characterize the neural source of attentional modulations, such as where and how top-down influences are generated. In contrast, our efforts to characterize the IPS as the source of top-down modulations provides an opportunity to study more directly the causes of modulations of sensory responses. Moreover, although some studies investigate only simple discrete manipulations of attention states (i.e., 'attend-in' or 'attend-out'), our measurements and results suggest that attentional effects

reflect a more complex set of factors.

One notable difference between the conventional CRFs and the ERFs here is that CRFs are usually calculated upon the responses of neurons whose receptive fields match presented stimuli. Here, to calculate ERFs we pool voxels who have diverse spatial tuning. We argue that such difference is unlikely the major driver of the effects here as pronounced attentional effects are found in high-level areas in which voxels have large receptive fields. Also, our results still hold in the category study where the CRFs are measured on FFA.

4.2. The flexible-attention framework

Cognitive tasks are diverse, imposing different task demands on neural processing. For example, the categorization task in the category study requires attention to the stimuli and decisions made upon them; the one-back task in the category study requires both attention and temporal maintenance of information. We propose a flexible-attention framework that postulates that attention enhances responses in task-relevant regions in order to process specific stimuli and meet certain task demands. This framework highlights the limitations of the conventional approach that is based solely on contrast response functions. Because cognitive tasks are remarkably diverse, using a fixed parametric form, as the conventional approach does, may overly simplify the neural processing of a task. However, it is still not entirely clear how to quantitatively generalize and predict responses under all possible stimulus conditions and attentional states. We do not suggest a specific mathematical function, and moreover, we emphasize that this is a *framework* that implies a change of conceptual stance, as opposed to a fully quantitative model of attention. Our framework can be viewed as a conceptual perspective on what types of questions might be fruitful to pursue in future research. In this framework, the observed top-down modulations in an experiment—which might be conventionally referred to as "attention"—depend on the details of the other cognitive processes used to fulfill the task (e.g.,

decision-making, memory). For example, the one-back task in the category study imposes additional memory demands than a simple spatial attention task. It has been known that detailed attentional manipulation, for example, different perceptual loads (de Haas et al., 2014), will evoke distinct neural activity patterns (Cukur et al., 2013; Nastase et al., 2017; Vaziri-Pashkam and Xu, 2017). During the digit task, while it was the experimental intention that spatial attention would be focused on the central digits, it is certainly possible that the sudden appearance of faces at peripheral locations may have produced some degree of bottom-up attentional drive. Thus, we acknowledge that exogenous attention may have influenced our measurements, and this may have reduced the observed differences between the digit task and the stimulus-directed tasks (dot and face tasks).

Some task-specific details might be missing in conventional fixed-parameter modeling approaches. One reason is that the studies using this approach to investigate relations between attention and contrast typically employ some standard experimental paradigms (e.g., spatial cueing tasks). To build a model one has to focus on a specific regime, stimulus, task, or experimental manipulation. Here, we instead use an alternative approach and tried to sample more stimulus dimensions and tasks. This approach can test more details in attentional processing. For example, even though attention can be allocated to two different stimuli in seemingly the same way, the task difficulty might differ for these stimuli and lead to differing neural effects (Kay and Yeatman, 2017; Ress et al., 2000). It is worth noting that some recent work extended conventional contrast response functions into neural network models, adding rich neural level mechanisms of attention (Lee and Maunsell, 2009; Miconi and VanRullen, 2016; Reynolds and Heeger, 2009). These studies are valuable as they make an important stride beyond merely using descriptive functions. Our work here is consistent with the spirit of these mechanistic models of attention.

Some previous studies are reminiscent of the concept of flexible attention. For example, the spatial tuning of neural populations can be flexibly altered according to the spatial focus of attention (Klein et al., 2014; Vo et al., 2017). Our emphasis is that not only does the spatial locus of attention influence neural activity, but the specific goal (or task context) engaged by the observer also matters. It has been previously shown that task difficulty in simple perceptual tasks imposes attentional effects on task-informative neural populations (Scolari et al., 2012; Scolari and Serences, 2009) and thus produces flexible cortical effects. The present study extends these previous results to task contexts that involve more complex cognitive processing (e.g., working memory). Also, we attempt to move beyond just the neural consequences of attentional modulation and attempt to make sense of the source of attentional effects at the network level (see the following section).

Note that we do not view task difficulty as a confound. Rather, how hard it is for a subject to execute a task may itself be part of the neural phenomenon that we are trying to characterize. We further analyze the behavioral data in the position study (see Supplementary Materials) and found that the influence of task difficulty on behavioral performance across eccentricities is quite small. Thus, task difficulty is relevant here but cannot be the simple explanation for our results.

The inverse relationship that we have demonstrated between the strength of bottom-up responses and the magnitude of attentional enhancement has a clear interpretation in the context of evidence-accumulation models of perceptual decision-making. Most visual tasks require the brain to accumulate sensory evidence to form a decision, and in general we may suppose that weak neural responses constitute weak sensory evidence, therefore leading to longer evidence-accumulation.

Note that the flexible-attention framework does not imply that weak neural responses *always* receive disproportionately large top-down modulation. If a task involves no demand for processing weak stimuli, the attentional effect on weak stimuli might be small. For an illustration, we found attentional effects to be relatively small for 0% phase-coherence stimuli (Fig. 6D–F). It may be the case that the absence of coherent form in these stimuli may render perceptual decisions (such as

category judgments or one-back judgments) easier compared to the case of partially coherent stimuli. Accordingly, the evidence-accumulation process may be quite short. To more definitively resolve these unknowns, it is necessary to develop formal characterizations of the decision-making and other cognitive processes that underlie task execution.

4.3. IPS as a potential source of top-down attentional enhancement

One might wonder how the flexible-attention framework could be used to quantitatively predict attentional effects given a known behavioral task. Indeed, the flexible-attention framework aims to propose an alternative treatment of attention other than the fixed-parameter approach. One idea is that if attentional effects depend on the task context (e.g., task difficulty), neural activity measurements signaling the task context could be used to predict the degree of attentional modulation. Following this idea, we proposed one such quantitative model, called the IPS-scaling model, in the category study (Kay and Yeatman, 2017). In that study, we demonstrated that IPS activity predicts the amount of task-induced response scaling observed in FFA and VWFA.

We explored whether this analysis can be extended to the data from the position study. As shown in Fig. 8A and B, IPS responses increase from the dot task to the face task, which mirrors the increase in top-down modulation in VTC from the dot task to the face task. However, we did not find systematic covariation between IPS activity and attentional modulation across stimulus eccentricities within a task. This is possibly due to experimental limitations. First, the position study did not set out to study interactions between IPS and VTC, and the scanning protocol provided only limited coverage of IPS (approximately up to IPS-0). This may have contributed to the noisy measurements of IPS responses (large horizontal error bars in Fig. 8A and B). Second, the experimental design of the position study might not have been optimal for eliciting strong responses from the IPS. This is because the very quick presentation of stimuli (500 ms/face) forces participants to quickly make decisions and this may preclude the complete unfolding of an evidence-accumulation process.

4.4. Stronger attentional effects in high-level visual areas

In the present study, we primarily focused on high-level category-selective visual regions instead of low-level or middle-level visual regions, which are typically the focus of previous studies. One benefit of choosing FFA and VWFA is that we have relatively advanced understandings of their functional selectivities (Grill-Spector et al., 2017). Moreover, these high-level visual areas are known for receiving greater attentional impacts compared to low-level visual areas (Kastner and Ungerleider, 2000). Indeed, we found much stronger attentional effects in high-level face-selective areas than low-level areas (Figs. 3 and 4). This provides a larger dynamic range of attentional enhancement, which helps to adjudicate different models of attention.

An important limitation of the analyses performed in this study is that we averaged responses across voxels in each low-level region (see Fig. 3). These averaged responses include many voxels that do not receive direct visual stimulation due to the strong retinotopic specificity of voxels in human early visual cortex. A more focused approach would be to strictly localize and analyze subpopulations of voxels that respond to stimuli at each eccentricity, as is common in classic studies of the effects of spatial attention in early visual cortex (Li et al., 2008; Murray, 2008). Thus, the quantifications performed in this study are not directly comparable to the results found in prior studies. Our results are presumably consistent with prior studies, in the sense that they provide a different view of the same underlying system. The primary motivation for the region-averaged approach is to provide a simple comparison for the results we find in ventral temporal cortex. Note that ventral temporal cortex has neuronal receptive fields that tend to be large and centered near the fovea (Desimone and Gross, 1979; Hasson et al., 2002; Rolls et al., 2003; Sato, 1989),

and thus is particularly well-suited for the region-averaged approach.

Another departure from previous studies is that we not only target high-level visual areas but also measure their responses to a wide range of stimulus and task manipulations. For instance, previous studies using the CRF modeling approach typically manipulate only stimulus contrast. How attention influences visual coding on a broader range of feature dimensions (e.g., eccentricity, phase coherence) remains understudied. In the position and category studies, we probed attentional effects as a function of three stimulus features (eccentricity, contrast, and phase coherence), providing a more complete characterization of functional properties of the visual system. One recent study found that attentional effects were larger in the fovea than in the periphery (Bressler et al., 2013). That study, however, used simple stimuli (i.e., checkboard) that elicited strong responses only in low-level visual areas. Another possibility is that attentional effects might depend on the retinotopic coverage of a brain area. FFA is known to over-represent visual fovea and attentional effects might be stronger on the less-represented locations (i.e., visual periphery). This account can be verified by exploring attentional effects in, for example, parahippocampal cortex, which tends to over-represent the periphery (Epstein and Baker, 2019). More broadly, one important direction for future work might be to compare differential attentional effects across low-level and high-level cortices using stimuli optimized for different areas.

4.5. Region-level characterization of attentional effects

The original analyses performed in the position study (Kay et al., 2015) examined attentional effects on spatial representation in human VTC at the level of single voxels. Through population receptive field (pRF) modeling, it was shown that task-specific attention alters the center, size, and amplitude of pRFs of voxels in VTC. This finding is consistent with several recent studies that characterize spatial tuning altered by attention in either the human or macaque brain (de Haas et al., 2014; Klein et al., 2014; Sheremata and Silver, 2015; Womelsdorf et al., 2006). One recent study suggested that the position shift of the pRFs towards visual periphery acts as the chief factor that promotes population codes (Vo et al., 2017).

The current paper performs a set of analyses that can be viewed as different from and complementary to the modeling of individual voxels. Specifically, we calculate region-level responses and investigate how and why the strength of attentional modulations varies for different stimuli and tasks. The approach here aims to directly contrast with the fixed-parameter approach to studying attention as performed in previous studies. Though the motivations are different, the two approaches have revealed conceptually consistent results. As the pRFs of individual voxels shift towards more peripheral locations, voxels exhibit stronger responses to peripheral stimuli. Thus, changes in voxel-level spatial preference are consistent with a region-level attentional enhancement that varies with eccentricity. This effect is particularly pronounced in high-level visual areas, such as FFA, but not in low-level areas, e.g., V1. ROI-based analyses and voxel-based analyses are certainly different and emphasize different aspects of population codes. They might yield seemingly different results; for example, pooling voxel responses within an ROI might dilute some voxel-specific effects. However, we highlight that both the ROI analyses presented here and the voxel-based analysis presented previously(Kay et al., 2015) demonstrate greater attentional effects in the face task compared to the dot task, and attentional effects are found to increase along the visual hierarchy. Note that this is not to say that attentional effects will always be minimal in low-level areas; low-level areas might exhibit strong effects for certain tasks and stimuli (see also (McMains and Somers, 2004)).

Overall, the two approaches are complementary and indeed attempt to analyze and interpret the same activity measurements, but they adopt very different theoretical frameworks. Both ways of thinking about the data are valuable.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.116964.

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