Differential impact of endogenous and exogenous attention on activity in human visual cortex

Laura Dugué[1,2,3,4], Elisha P. Merriam[1,2,5], David J. Heeger[1,2] & Marisa Carrasco[1,2]

[1] Department of Psychology, New York University
[2] Center for Neural Science, New York University
[3] Université de Paris, CNRS, Integrative Neuroscience and Cognition Center, F-75006 Paris, France
[4] Institut Universitaire de France, Paris, France
[5] Laboratory of Brain and Cognition, NIMH/NIH, Bethesda, MD

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Corresponding author:
Laura Dugué
Current address: 45 rue des Saints-Pères 75006 Paris, FRANCE
laura.dugue@u-paris.fr

ABSTRACT (148 words)

How do endogenous (voluntary) and exogenous (involuntary) attention modulate activity in visual cortex? Using ROI-based fMRI analysis, we measured fMRI activity for valid and invalid trials (target at cued/un-cued location, respectively), pre- or post-cueing endogenous or exogenous attention, while participants performed the same discrimination task. We found stronger modulation in contralateral than ipsilateral visual regions, and higher activity in valid- than invalid-trials. For endogenous attention, modulation of stimulus-evoked activity due to a pre-cue increased along the visual hierarchy, but was constant due to a post-cue. For exogenous attention, modulation of stimulus-evoked activity due to a pre-cue was constant along the visual hierarchy, but not modulated due to a post-cue. These findings reveal that endogenous and exogenous attention distinctly modulate activity in visuo-occipital areas during orienting and reorienting; endogenous attention facilitates both the encoding and the readout of visual information whereas exogenous attention only facilitates the encoding of information.

Keywords: exogenous attention, endogenous attention, fMRI activity, occipital visual areas, top-down processing, bottom-up processing.

INTRODUCTION

Spatial, covert visual attention is the selective processing of visual information in space, without change in gaze. Attention can be allocated voluntarily –endogenous attention– or involuntarily –exogenous attention. Endogenous and exogenous attention have different temporal dynamics; endogenous takes about 300 ms to be deployed and can be sustained at will whereas exogenous attention takes only about 100 ms to be deployed and it is transient (for review see [1,2]). These two types of attention often have similar perceptual consequences (reviews by [1,2]), but notable exceptions indicate that whereas endogenous attention acts in a flexible way, exogenous attention acts in an inflexible or automatic way. For instance: (a) The benefits and costs in perception (discriminability and speed of information accrual) scale with cue validity for endogenous but not for exogenous attention (e.g. [3]); (b) The effects of covert attention on contrast sensitivity often differ for endogenous and exogenous attention (e.g. [4-7]); and (c) For a texture segmentation task in which heightened spatial resolution improves or impairs performance as a function of target eccentricity, endogenous attention improves performance across eccentricity, whereas exogenous attention improves performance at peripheral locations where resolution is poor, but hampers performance where resolution is already high for the task at hand (e.g. [8-12]).

Basic visual processes, such as contrast sensitivity and spatial resolution, are mediated by activity in early visual cortex, and are altered by covert attention (reviews by [1,2,13,14]). Specifically, single-unit studies in monkeys have demonstrated effects of endogenous attention in occipital areas (e.g. [15-22]). Additionally, fMRI studies have shown that endogenous attention causes a baseline shift in early visual areas (e.g. [23-29]; review by [30]) and increases the dynamic range of fMRI responses [31,32]. Comparatively, little is known about the effect of exogenous attention on visual areas both from single-unit studies [33,34] and fMRI studies (for reviews see [1,13]).

Since Corbetta and Schulman's seminal review (2002) [35] on the neural bases of endogenous and exogenous attention, there has been emphasis on characterizing networks of brain regions within the frontal and parietal lobes (for reviews see [30,36,37]). Yet, there remains considerable debate regarding the dissociation between dorsal regions, for endogenous attention, and ventral regions, for exogenous attention (e.g. [37,38]), including the role of the temporo-parietal

junction (TPJ; [39-42]). Classically, researchers have described endogenous attention as a top-down process, and exogenous attention as a bottom-up process [1,35,37,43-45]. This characterization originated in psychophysics experiments, and was then studied using fMRI, in which the two types of attention have been often investigated separately (for reviews [1,30,36,43]).

Studies of endogenous and exogenous attention focusing on parietal and frontal areas have shown that the two types of attention differentially modulate fronto-parietal connectivity [37,46]. For example, there are critical differences in the temporal order of neural responses in frontal and parietal cortex in monkeys between these attention conditions, i.e. frontal activity precedes parietal activity during endogenous attentional orienting, whereas parietal activity precedes frontal activity during exogenous orienting. Critically, it is often assumed that the effects of endogenous and exogenous attention are the same in striate and extra-striate areas [30,35,36,47,48].

A number of important considerations limit the conclusions that may be drawn from the few studies that have directly compared independent effects of visual exogenous and endogenous spatial attention [37,48-50]:

(1) The effect of attention on behavioral performance was assessed in some studies with a detection task using RT as their only dependent variable [48,50], in which performance may differ due to speed of processing, discriminability or criterion [51-53] and/or motor behavior [54,55].

(2) In the studies in which performance was assessed in a discrimination task using RT [49], small RT differences were reported, which could have resulted from speed of processing, discriminability, or criterion factors [51-53].

(3) In the studies in which accuracy was not assessed [37,48,50], it is not possible to know whether task difficulty was the same for both types of attention, and task difficulty can interact with the strength of fMRI activity [56,57].

(4) For the studies in which eye position was not monitored while participants performed the task in the scanner [37,48-50], the results could be due to covert attention, overt attention or both [1,58,59].

(5) Given that exogenous attention is a fast, transient process (for review see [1,2]), it was inappropriately manipulated in the studies in which long stimulus onset asynchronies (SOA) were used [48,49,60,61 62] making the comparison between the two attention conditions problematic.

(6) Except for two studies, one interested in attentional modulation in the Fusiform Face Area (FFA) [61] and the other in the TPJ [39], statistical parametric mapping was applied to group averaged data to identify regions of the brain that were active during task performance. Some found significant activity in the occipital pole [48-50], but attentional modulation of fMRI activity was not systematically assessed across different visual areas.

Given all these methodological limitations, it is unknown how these two types of attention affect neural activity in each individual visuo-occipital area, and how modulation of activity in visual cortex is linked to changes in perceptual performance. (See Dugué and colleagues [39], who published a table summarizing these and other methodological problems for studies regarding covert attention and TPJ activation).

Typically, covert attention is manipulated by presenting a pre-cue, prior to the target –and the aforementioned studies also did so (see **Table 1**). However, endogenous post-cues, presented after target offset, can also improve performance by affecting the information readout [63-66] and modulate fMRI activity in early visual areas [23,65-67]. Exogenous post-cues also affect performance in some tasks [68,69], but not in others [70-73], and the only fMRI study evaluating post-cues in exogenous attention showed no such modulation [74]. Critically, no single study has compared visual cortex activity with post-cues in endogenous and exogenous attention.

Study	Cueing manipulation		Task	Dependent Variable	Analysis	Cortical areas	Eye tracking	Correlation MRI-behavior
	Endogenous	Exogenous						
Studies including Occipital areas								
Detection tasks								
50	central arrow 70% valid	luminance change of peripheral placeholder 50% valid	X	RT	Group-averaged	**Occipital:** *Cuneus, MOG, SOG* + Frontal Temporo-Parietal	No	No
	SOA=100 or 800 ms							
48	central arrow 75% valid	brightening of peripheral placeholder 50% valid	square	RT	Group-averaged	**Occipital:** *Cuneus* + Frontal Temporo-Parietal	No	No
	SOA=550 ms							
62	single peripheral rectangular frame 100% valid	five peripheral rectangular frames 20% valid	a black and white checkerboard	RT *for 4 out of 8 participants*	Group-averaged	**Occipital:** *Fusiform, TOS, LG, SC, LOG* + Frontal Temporo-Parietal	No	No
	SOA=8, 8.15, 8.3, 8.45 or 8.6 s							
Discrimination tasks								
49	brightening of half of central fixation diamond 75% valid	color singleton in an array of colored squares 50% valid	T vs. L	RT (% correct)	Group-averaged	**Occipital:** *LO, MT, Cuneus, Fusiform, SOG* + Frontal Temporo-Parietal	No	No
	SOA=2160 ms							
61	color change of a peripheral placeholder 75% valid	50% valid	face identity	RT (% correct)	ROI-based (FFA) + Group-averaged	**Occipital:** *FFA* + Frontal Temporo-Parietal	Yes	No
	SOA=300 ms							
Current study	central bar 75% invalid SOA=310 ms	peripheral bar 50% valid SOA=110 ms	orientation	d-prime (RT)	ROI-based	**Occipital:** *V1, V2, V3, V3A, hV4, LO1*	Yes	Yes
Studies NOT including Occipital areas								
Detection tasks								
60	central arrow 80% valid	peripheral dot 50% valid	filling of a square	RT	Group-averaged	Frontal Temporo-Parietal	No	No
	SOA=400, 550 or 700 ms							

Discrimination tasks								
75	thickening of part of central fixation diamond 80% valid SOA=200, 400 or 800 ms	luminance change of peripheral placeholder 50% valid SOA= 100, 150 or 200 ms	X vs. +	RT (% correct)	Group-averaged	Frontal Temporo-Parietal	No	No
76	color change of central fixation 83% valid SOA=700–1000 ms	whitening of peripheral placeholder 50% valid SOA=100–300 ms	central color of a checkerboard	Inverse efficiency = RT/%correct	Group-averaged	Frontal Temporo-Parietal	No	No
39	central bar 75% invalid SOA=310 ms	peripheral bar 50% valid SOA=110 ms	orientation	d-prime (RT)	ROI-based	Temporo-Parietal	Yes	No
37	color change of central fixation 83% valid SOA=700–1000 ms	whitening of peripheral placeholder 50% valid SOA=100–300 ms	central color of a checkerboard	Inverse efficiency = RT/%correct	Group-averaged	Frontal Temporo-Parietal	No	No

Table 1. fMRI studies comparing endogenous and exogenous attention independently in human participants. *For each study, we report the cueing manipulation for each attention condition (SOA: Stimulus Onset Asynchrony is the duration of the cue + interval before onset of the target), the task performed by the participants, the dependent variable reported in the publication, whether the analysis was based on group-averaging or ROI-based on single-participants, the cortical areas reported in the publications and showing significant activation due to cue and/or target, whether or not eye data were monitor in the scanner or used for the subsequent fMRI analysis, and whether the fMRI BOLD signal was correlated with behavioral measures. IOG: Inferior Occipital Gyrus; LG: Lingual Gyrus; LO: Lateral Occipital area; LOG: Lateral Occipital Gyrus; MOG: Middle Occipital Gyrus; MT: Middle Temporal area; SC: Striate Cortex; SOG: Superior Occipital Gyrus; TOS: Temporal-Occipital Sulcus.*

Here, with the same participants, task, stimuli and task difficulty for all attention manipulations, we tested the following four predictions: (1) Pre-cueing should induce an attentional modulation of fMRI activity (e.g. [74]), higher in the valid than the invalid condition in which attention needs to be reoriented to the opposite location (e.g. [39,47,77,78]) to perform the task. (2) Both endogenous and exogenous pre- and post-cueing effects should be stronger in visual regions contralateral to the attended hemifield (e.g. [23,74]). (3) Pre-cueing endogenous attention, but not exogenous attention, should increase activity modulations along the visual hierarchy (e.g. higher in V4 than in V1; [23,28]; for reviews [30,36]). For endogenous attention, a top-down process, modulations from higher-order, fronto-parietal attentional regions would send feedback information to visual cortex with diminishing effects in earlier visual areas [28,29,36,79-82]. (4) Post-cueing endogenous [23,65-67], but not exogenous [74], attention should induce attentional modulation of fMRI activity in early visual areas. Voluntary, endogenous attention would facilitate reading out perceptual information [39], and modulate its processing [23,65-67]. The only fMRI study assessing the effects of post-cueing exogenous attention found no attentional modulation of fMRI activity in early visual areas [74]; some behavioral studies report post-cueing effects [68,69] but others found no such effects [70-73].

To test these four predictions, we measured fMRI activity and compared the effects of endogenous and exogenous attention in early visual areas while the same participants performed the same task –a 2-AFC orientation discrimination task, contingent upon contrast sensitivity [4,83,84]. We used a fully-crossed design: two attention conditions –endogenous or exogenous attentional orienting– and two types of cueing –pre- or post-cue. We evaluated fMRI activity at both the attended and the un-attended locations, given the ubiquitous performance tradeoffs at attended (benefits) and unattended (costs) locations compared to a neutral condition (e.g. [3,25,85-89]), and the importance of evaluating both the orienting and reorienting of attention [39,77,90], critical in an ever-changing environment [77,91].

This is the first study to systematically evaluate and directly compare how pre and post-orienting, and reorienting, of endogenous and exogenous attention modulate neural activity in visual cortex to affect behavior. The results indicate that these two types of spatial covert attention distinctly modulate activity in individual retinotopic visual cortical areas. These differences in

activity are consonant with differential engagement of top-down and bottom-up processes and their respective temporal dynamics. These results suggest that endogenous attention facilitates both the encoding and the readout of visual information whereas exogenous attention only facilitates the encoding of information.

RESULTS

Endogenous and exogenous attention improve performance

Participants performed a 2-AFC orientation-discrimination task under two attentional conditions (exogenous or endogenous attention), when the cue was presented either before (pre-cue) or after (post-cue) the grating stimuli (see Methods), and while their brain activity was measured with fMRI (**Figure 1**).

In each condition, we calculated performance accuracy (d'), as the main dependent variable, for each participant separately (**Figure 1B**, top row). A three-way repeated measures 2x2x2 ANOVA (exogenous/endogenous x valid/invalid x pre/post-cue) revealed higher performance for valid than invalid cues ($F(1,4)=23.6$, $p=0.008$), that exogenous and endogenous cues were statistically indistinguishable ($F(1,4)<1$), and that there was no significant difference between pre- and post-cues ($F(1,4)<1$). All the two and three-way interactions were not significant ($F<1$).

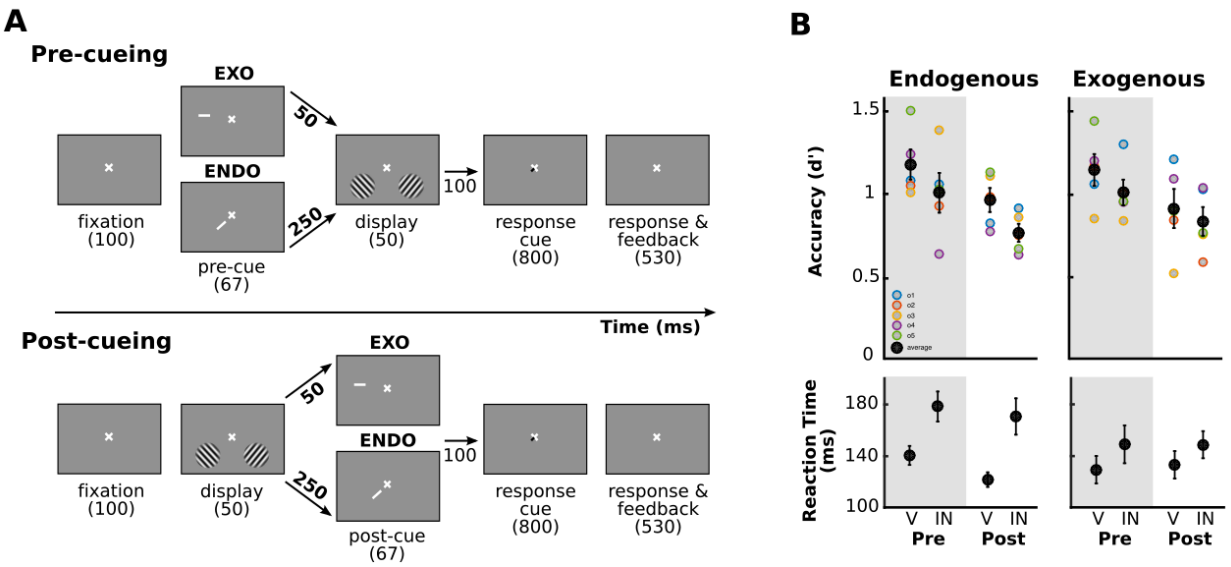

Figure 1. Experimental protocol. A. *Participants performed a 2-AFC orientation-discrimination task. Pre-cues and post-cues were presented before and after the stimuli, respectively.*

Exogenous cues appeared in the periphery, above one of the two stimulus locations. Endogenous cues appeared at the center of the screen (the display is not at scale for visibility purposes) and indicated one of the two stimulus locations The ISI between the cue and the gratings was shorter for the exogenous (50 ms) than the endogenous (250 ms) conditions. A response cue indicated the target location and instructed participants to indicate whether the target grating was tilted clockwise or counterclockwise of vertical by pressing one of two keys. To provide feedback, the fixation-cross turned green or red for a correct or an incorrect answer, respectively. ***B.*** *Behavioral performance averaged across participants (black dots) and for each of them (colored dots; n=5) for endogenous (left) and exogenous (right) attention. (Top) Performance accuracy (d'; top) and median reaction time (bottom) as a function of cueing condition. V, valid cue (same location of pre-cue/post-cue as response cue). IN, invalid cue (different location of pre-cue/post-cue than response cue). Pre, pre-cue presented before the stimuli. Post, post-cue presented after the stimuli. Valid cues induced more accurate and faster responses (there was no speed-accuracy trade-off). Error bars, ± 1 SEM across participants.*

In each condition, we also calculated reaction time, as a secondary dependent variable (note that the task is not optimize for reaction time's effect due to the long response cue window during which participants are not allowed to provide their response), for each participant separately (**Figure 1B**, bottom row). A three-way repeated measures ANOVA revealed faster reaction times for valid than invalid cues ($F(1,4)=62.3$, $p=0.001$). There was no significant difference between exogenous and endogenous cues ($F(1,4)=2.7$, $p=0.17$), or between pre- and post-cues ($F(1,4)=1.7$, $p=0.27$). Two significant interactions indicated that the differences between valid and invalid cues ($F(1,4)=16.2$, $p=0.02$) and between pre- and post-cues ($F(1,4)=8.1$, $p=0.047$) were more pronounced for endogenous attention than for exogenous attention.

These behavioral results, which are consistent with previous findings [3,4,6,25,84,86,92], show that attention improved orientation discrimination (d' and reaction time), with no evidence of a speed-accuracy trade-off, and similarly for both types of attention and for both pre- and post-cues. Thus, the behavioral effects confirm the successful manipulation of endogenous and exogenous attention, for both pre- and post-cues, consistently across individuals.

Attentional modulation of perceptual and post-perceptual information processing in visual cortex

Visual areas were mapped in each participant following retinotopic mapping procedures (**Figure 2**, left panel) and a targeted stimulus localizer (**Figure 2**, right panel), and regions of interest (ROIs) were selected based on previous literature: V1, V2, V3 (for V2 and V3, ventral and dorsal ROIs were averaged), V3A, hV4 and LO1 (e.g. [93-96]).

Activity was higher for contralateral than ipsilateral brain areas. For each ROI, we measured the fMRI response amplitudes for each type of attention – exogenous and endogenous – and each cueing condition – pre- and post-cueing, for the contralateral and ipsilateral side to the cued (attended) location. We analyzed the fMRI responses evoked by each type of attention in the contralateral and ipsilateral brain regions relative to the cue location (**Supplemental Figure 1**). ANOVAs indicated that there was higher contralateral than ipsilateral activity across brain areas (endogenous: $F(1,4)=59.9$, $p=0.0015$; exogenous: $F(1,4)=218.8$, $p=0.0001$). For both types of attention, this difference was more pronounced for valid than invalid cues (endogenous: $F(1,4)=8.6$, $p=0.04$; exogenous: $F(1,4)=21.1$, $p=0.01$). In the following analyses, we then concentrate on fMRI activity in the contralateral ROIs to the attended location.

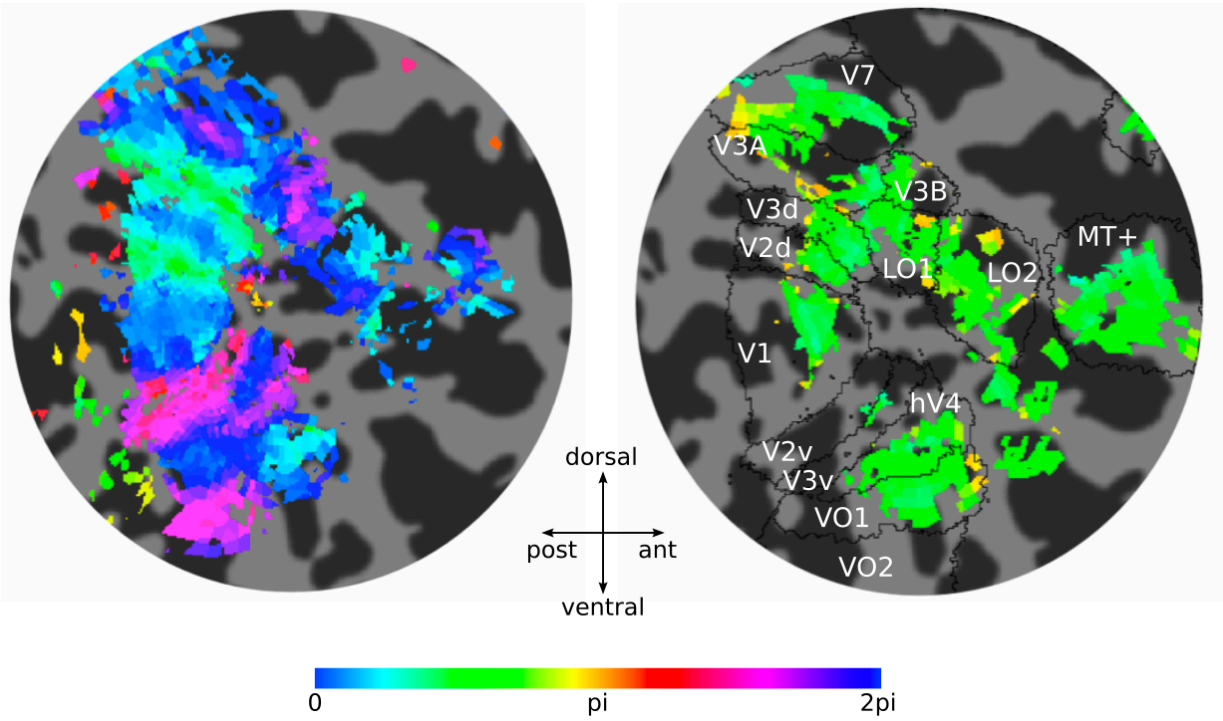

Figure 2. Retinotopic mapping and stimulus localizer of a representative participant. *A flattened representation of the right hemisphere occipital pole.* ***Left,*** *map of polar angle. The color of each voxel in the map represents the response phase of the time series elicited by a rotating wedge stimulus.* ***Right,*** *stimulus localizer. The black outlines correspond to the retinotopic areas (defined for each participant based on their polar angle maps). The color of each voxel indicates the phase of the response to the grating stimuli presented in the lower left visual field.*

fMRI responses correlated with behavioral variability. We evaluated the degree to which inter-individual variability in behavioral performance co-varied with variability in fMRI responses.

We computed the correlation (**Figure 3A**), across participants, ROIs, types of attention and cueing conditions, between the fMRI responses (percent change in image intensity) and behavioral performance accuracy (d'). We found a positive correlation between fMRI activity and d' (Pearson correlation r = 0.23, p = 0.003), which was present for both attention types (endogenous: Pearson correlation r = 0.3, p = 0.003; exogenous: r = 0.2, p = 0.02). We further showed that fMRI activity was overall higher for valid than invalid trials (t(4) = 4.0, p = 0.0163, Cohen's d = 1.78). This was the case for each participant (**Figure 3B**). Together, these results are consistent with previous findings showing that fMRI response correlates with behavioral variability [97-99], and that attentional orienting increases fMRI signal in early visual cortex (for review [30]).

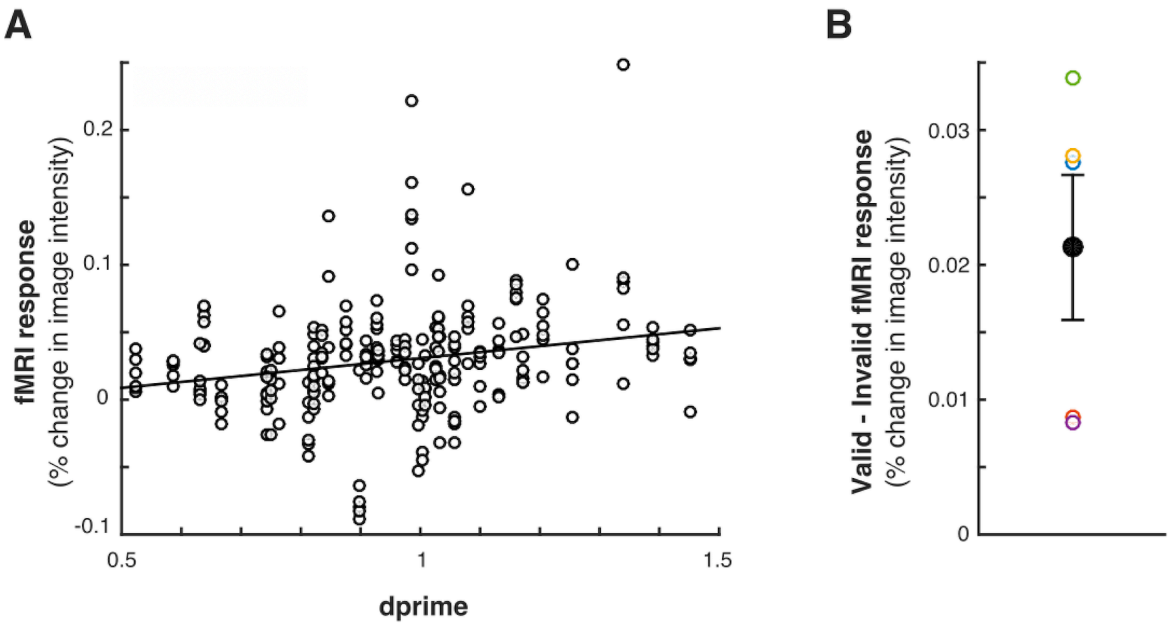

Figure 3. Inter-individual fMRI response. A. *Positive correlation between fMRI response and behavioral performance (Pearson correlation r = 0.23, p = 0.0003). Each dot indicates fMRI response amplitude measured from one ROI and one participant, separately for each attentional condition (pre and post-cue, valid and invalid).* ***B.*** *fMRI response difference between valid and invalid trials combined across all conditions and ROIs for each participant (colored dots), and across participants (black dot; average significantly positive: t(4) = 4.0, p = 0.0163, Cohen's d = 1.78). Error bar, ± 1 SEM across participants.*

We then tested our two novel predictions: (1) attentional modulation of fMRI stimulus-evoked activity increases along the visual hierarchy for endogenous pre-cueing, but is constant for exogenous pre-cueing; and (2) attentional modulation of fMRI stimulus-evoked activity for endogenous post-cueing is constant along the visual hierarchy, whereas there is no attentional

modulation for exogenous post-cueing. We measured the differences in activity between valid and invalid trials for each type of attention and for pre- and post-cues, across the hierarchy of visual cortical areas. fMRI responses were significantly larger for valid than invalid cues, for both endogenous and exogenous cues, and for both pre- and post-cues. A three-way repeated measures ANOVA (2 exogenous/endogenous x 2 pre/post-cue x 6 ROIs) of the difference between valid and invalid conditions revealed significant main effects of exogenous/endogenous condition ($F = 10.0$, $p = 0.0341$) and of ROI ($F = 5.5$, $p = 0.0024$), as well as an interaction between pre/post-cue and ROI ($F = 4.1$, $p = 0.0103$). Thus, we investigated modulations of fMRI activity separately for pre and post-cueing attention conditions.

Linear mixed models [100] were then used to test our main predictions; namely (1) increase of fMRI activity along the visual hierarchy for pre-cueing endogenous attention but not exogenous attention, and (2) post-cue attentional modulation of fMRI activity for post-cueing endogenous attention but not exogenous attention. We implemented two models, one for the pre-cueing and the other for the post-cueing condition, to test the link between fMRI activity and the interaction between ROI and endogenous/exogenous attention conditions. In each model, we entered as fixed effect the ROI and the endogenous/exogenous conditions into the model, as well as their interaction. As random effects, we had participant's intercepts and slopes for the effect of ROI and endogenous/exogenous conditions. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. P-values were obtained by likelihood ratio tests. For the pre-cueing condition, we observed a significant effect of ROI ($t(56)=3.8$, $p=0.0004$, estimate=0.02±0.005, standard error), as well as a significant interaction between ROI and endogenous/exogenous conditions ($t(56)=-2.4$, $p=0.018$, estimate=-0.007±0.003, standard error). For the post-cueing condition, we observed a significant effect of the fixed effect intercept ($t(56)=2.2$, $p=0.03$, estimate=0.04±0.02, standard error). Finally, we performed independent regression analyses on each pre-/post-cueing and endogenous/exogenous attention conditions (**Figure 4**). We observed a significant increase along the hierarchy of the visual areas of the activity difference evoked by valid and invalid trials for the endogenous pre-cueing condition ($F = 25.8$, $p = 0.007$, $R^2 = 0.87$), but not for the exogenous pre-cueing condition ($F = 2.8$, $p = 0.168$,

R^2 = 0.41), endogenous post-cueing (F = 3.0, p = 0.161, R^2 = 0.42) or exogenous post-cueing conditions (F = 0.1, p = 0.774, R^2 = 0.02).

Together, the results of the linear mixed models and the regression analyses (**Figure 4**) showed differential effects between pre-/post-cueing and endogenous/exogenous attention conditions. The difference in fMRI activity between valid and invalid trials increases along the hierarchy of the visual areas in pre-cueing of endogenous attention but not of exogenous attention. Moreover, there is a difference in fMRI activity between valid and invalid trials with post-cueing of endogenous attention that is constant along the hierarchy (significant intercept), but absent for post-cueing of exogenous attention. These analyses are consistent with post-hoc t-tests performed for each condition and ROI (**Figure 5**).

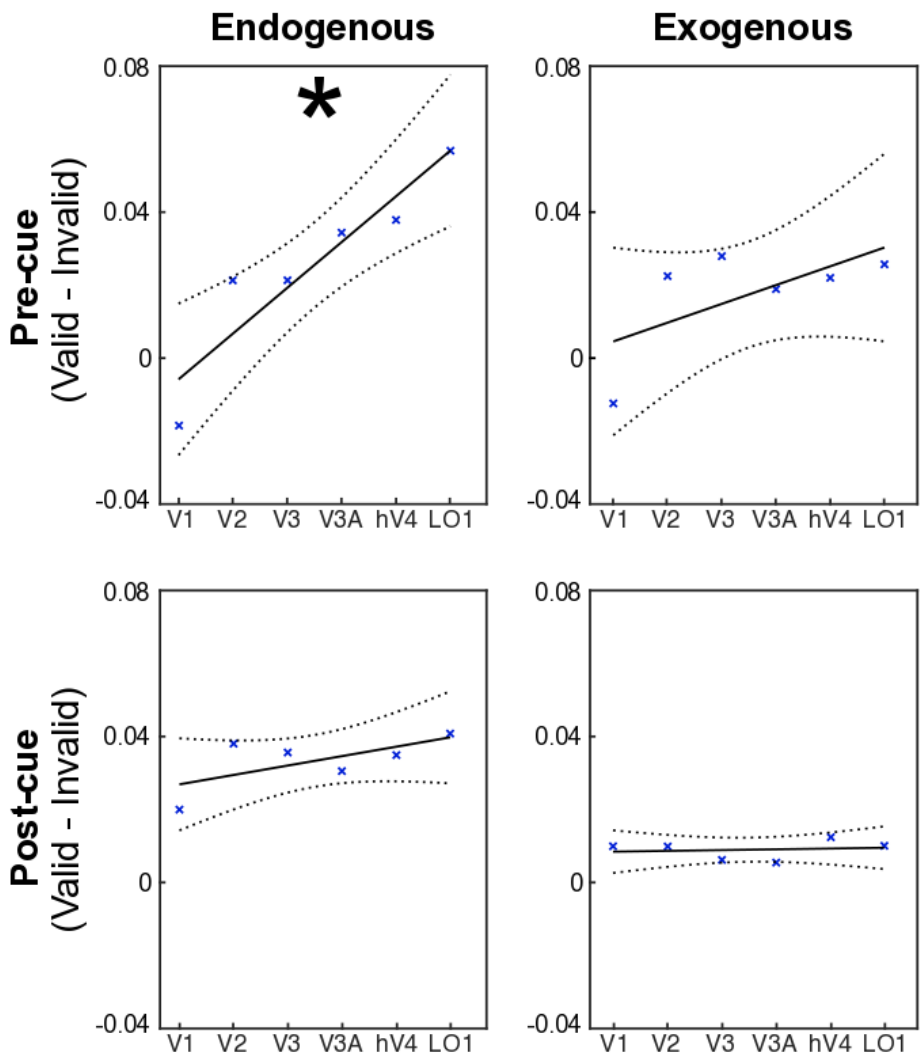

Figure 4. Specificity of pre and post-cueing for endogenous and exogenous attention. *The difference in fMRI response between valid and invalid is plotted separately for pre- and post-cue conditions for each ROI. *, Statistically significant regression analysis (p < 0.05).*

For both endogenous attention ($p < 0.05$ for V3a, V4 and LO1; trend ($p = 0.077$) for V3; t-tests) and exogenous attention ($p < 0.05$ for V3, V3A, hV4 and LO1; trend ($p = 0.074$) for V2; t-tests) pre-cues elicited greater fMRI activity for valid than invalid cues (**Figure 5**, top-left and top-right panels). Furthermore, for endogenous attention ($p < 0.05$ for V2, V3, V3A, hV4 and LO1; trend ($p = 0.077$) for V1; t-tests; **Figure 5**, bottom-left panel), but not for exogenous attention (all $p > 0.1$; t-tests; **Figure 5**, bottom-right panel), post-cues elicited greater fMRI activity for valid than invalid cues in occipital areas (detailed statistics are presented in Supplementary Table 1). Critically, these effects were consistently observed across participants (**Figure 6**). Taken together, these results confirm both of our predictions.

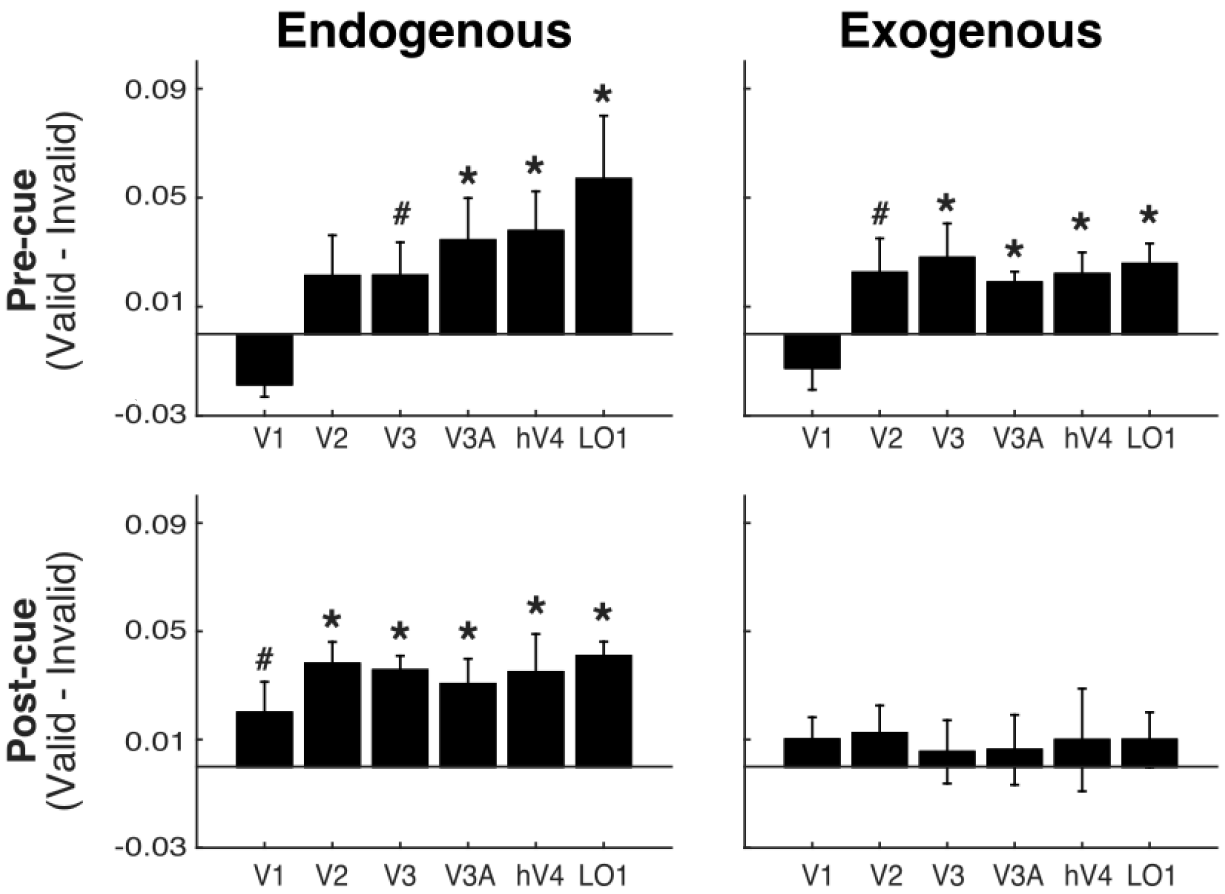

Figure 5. Single ROI responses for pre and post-cueing and for both endogenous and exogenous attention. *The difference in fMRI response between valid and invalid is plotted separately for pre and post-cue conditions for each ROI (same data as in Fig 4). *, Statistically significant difference between valid and invalid, separately for pre and post-cueing ($p < 0.05$). #, trend ($p < 0.1$). Error bars on plots are ± 1 SEM.*

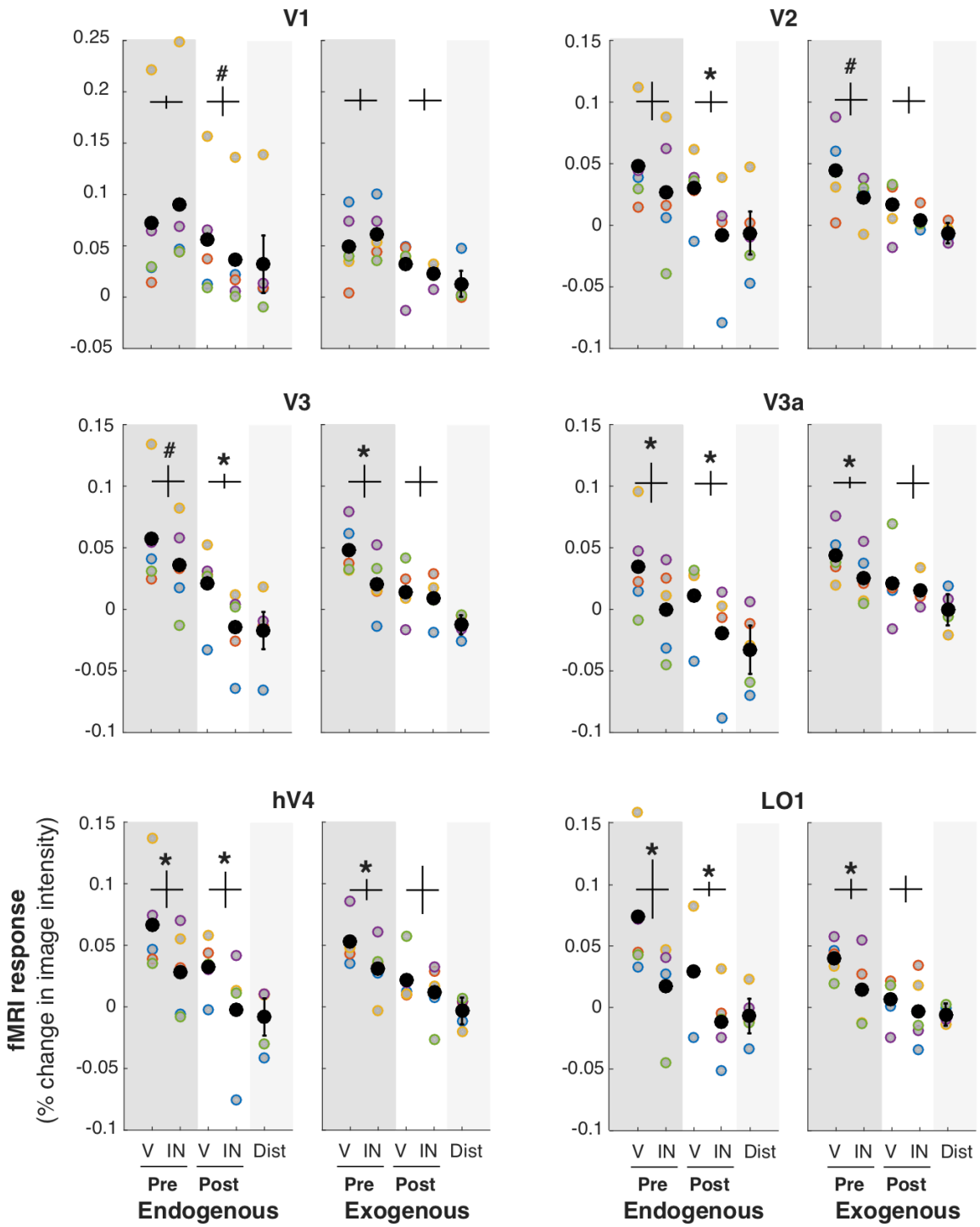

Figure 6. Specificity of each visual ROI for endogenous and exogenous attention. *fMRI response amplitude was measured for each attentional condition. V: valid cue condition (target location matches the location indicated by pre-cue/post-cue). IN: invalid cue condition (target location at the opposite location relative to the pre-cue/post-cue). Pre: pre-cue presented before the grating stimuli. Post: post-cue presented after gratings. All four conditions in the contralateral ROI. Distractor (Dist): all conditions averaged in the ipsilateral ROI. Each colored point corresponds to the data of one participant. The black points represent the average across all 5 participants. *, Statistically significant difference between valid and invalid, separately for pre and post-cueing ($p < 0.05$). #, trend ($p < 0.1$). Detailed statistics are presented in Supplementary Table 1. Error bars (vertical lines) are plotted on the difference between valid and invalid and represent ± 1 SEM across participant.*

DISCUSSION

This is the first study to compare pre and post-orienting, and reorienting, of endogenous and exogenous attention in visual cortex, while concurrently assessing visual performance using well-established psychophysical protocols to manipulate attention. The fact that the same participants performed the same orientation discrimination task with the same stimuli and task difficulty under different attentional manipulations enabled us to isolate the fMRI activity induced by each type of attention during orienting and reorienting.

Previous studies comparing endogenous and exogenous attention conditions state various attentional effects in early visual areas (see **Table 1**). Some report differential effects between these attention conditions in the right LO and MT [49], others in the cuneus [48-50], the occipital gyrus (SOG, MOG, LOG; [49,50,62]), the fusiform area [49,61,62], and the TOS, LG and SC [62]. This lack of clear picture regarding the differential impact of endogenous and exogenous spatial attention is likely due to the methodological differences and limitations we discussed in the Introduction (see also **Table 1**). In any case, it is often assumed that the effects of endogenous and exogenous attention are the same in visual occipital areas [30,35,36,47,48].

To further our knowledge of the neural correlates of attention, we investigated both attentional orienting (valid cueing) and reorienting (invalid cueing), critical in an ever-changing environment [77,91]. Furthermore, given ubiquitous performance tradeoffs between attended (benefits) and unattended (costs) locations (e.g. [3,25,87,88]), we assessed activity at both attended (contralateral ROI) and unattended (ipsilateral ROI) locations. Finally, we investigated how attentional effects varied as a function of pre- and post-cueing, thus contrasting the neural correlates of perceptual and post-perceptual processing of information.

There was an overall positive correlation between performance in the orientation discrimination task and the degree of attentional modulation in fMRI activity. This result was expected, indicating that as discriminability increases so does the attentional modulation in fMRI activity. But only very few studies on the effect of spatial attention in early visual areas have reported such a correlation [97-99]. The behavioral effects obtained in the scanner are consistent with psychophysical studies. The enhanced performance brought about by the valid, but uninformative

347 peripheral pre-cue is consistent with an automatic, bottom-up involuntary capture of exogenous
348 attention (e.g. [3,6,25,87,101]). The enhanced performance brought about by the valid, informative cen-
349 tral precue is consistent with a top-down, voluntary deployment of endogenous attention (e.g.
350 [3,6,25,102,103]).

351 In the endogenous attention condition, there was an increase in attentional modulation of
352 stimulus-evoked activity along the hierarchy of visual areas. There is no consensus regarding the
353 visual hierarchy beyond area V3 (e.g. [104-108]), especially regarding V3A. However, most authors
354 agree that hV4 precedes LO1 [104-107]. In any case, our data are consistent with either a strict
355 hierarchy or with V3A and hV4 being at the same level. Such a pattern is consistent with previous
356 studies suggesting that endogenous attention is a top-down modulation from frontal and parietal
357 areas feeding back to visual cortex, with diminishing effects in earlier visual areas [28,36,79,80]. In-
358 consistent with previous studies (e.g. [23,25,29,109,110]), there was no evidence for attentional modu-
359 lation in V1. It might be that attentional modulation of V1 activity is more variable than other visual
360 cortical areas, making it harder to detect (see also [28,74]). Methodological differences between this
361 and previous studies may have contributed to weakening the effect of attention in V1. The accrual
362 time in the current endogenous condition was relatively short (1300 ms in the valid condition and
363 500 ms in the invalid condition) compared to previous studies investigating endogenous, volun-
364 tary attention, in which the cue and/or stimuli were presented for a long duration to maximize
365 BOLD measurements (e.g. [23,29,109,110]). We chose the minimum SOA (317 ms) at which perfor-
366 mance benefits plateau to have as comparable conditions as possible to the accrual time with
367 the SOA for exogenous attention (117 ms). This short accrual time may have limited the effects
368 of attentional feedback to V1.

369 In the exogenous attention condition, in contrast to the endogenous attention, the atten-
370 tional modulation was approximately constant across the visual hierarchy. Some previous studies
371 have reported a similar effect [111,112], others a decrease [113], and yet others an increase [74,114] across
372 the visual areas. This difference might be explained by different task parameters. For example,
373 in the Liu et al. (2005) study [74], participants knew which of the two stimuli was the target they had
374 to discriminate while the stimuli were presented, as one stimulus was vertical and the other was

375 tilted to the left or the right. In the present study, both stimuli were independently tilted and par-
376 ticipants had to wait for the response cue to appear to know which one was the target and which
377 one was the distractor.

378 Unlike in the endogenous pre-cueing condition in which the attention effect increased along
379 the processing stream, for the endogenous post-cueing effect there was no evidence that it varied
380 across these visual areas. The constant effect in the post-cue condition could be due to the con-
381 tribution of two counteracting factors: (1) the fMRI response evoked by the stimulus in early visual
382 areas may decrease along the visual hierarchy [115]; (2) the top-down modulations from frontal and
383 parietal areas feedback to visual cortex with diminishing effects in earlier visual areas [23,28,116].

384 In the exogenous condition, there was no significant post-cueing effect on early visual ar-
385 eas. This result is consistent with that of Liu et al. (2005) [74], who while evaluating exogenous
386 attention effects on occipital cortex included a post-cue condition to rule out sensory contamina-
387 tion of the cue (i.e. sensory response evoked by the cue itself) contributing to the enhanced
388 BOLD activity found in their pre-cue condition. In addition to ruling out a possible sensory con-
389 tamination, the present results show that, in contrast to endogenous attention, exogenous atten-
390 tion does not aid in the selective readout of information.

391 The ROI-based analysis that we followed here enabled us to compare contralateral and
392 ipsilateral modulation of BOLD activity, thus providing additional information regarding the differ-
393 ences in processing dynamics of both types of attention. We observed a larger difference be-
394 tween contralateral and ipsilateral areas for the valid than the invalid cueing condition. This effect
395 could be due to the fact that for the former, participants were attending to the same location
396 throughout the trial, whereas for the latter, when the response cue did not match the pre-cue,
397 participants had to switch their spatial attention to the opposite stimulus location, thus activity at
398 that new location would be accumulated for less time. For instance, for endogenous attention, for
399 the valid condition participants had been processing the target for almost 500 ms before the
400 response cue appeared. When the response cue matched the pre-cue, participants continued
401 processing and reading out the signal from that location for up to 800 ms (they were not allowed
402 to give an answer before the end of the response cue period). But when the response cue did

not match the pre-cue, then participants had to switch after 500 ms to the other location (ipsilateral) thus accumulating less activity. Similarly, the accumulation time for the invalid cue condition in exogenous attention was only about 300 ms. This accrual time explanation could also account for the larger difference between contralateral and ipsilateral for pre-cues than post-cues, i.e. there is a 300 ms accumulation when the exogenous pre-cue is invalid, while only 100 ms when the post-cue in invalid. Likewise, the larger modulatory effect for endogenous relative to exogenous attention is consistent with the difference in accrual time.

In a recent study [39] we demonstrated that sub-regions of the Temporo-Parietal Junction (TPJ) that respond specifically to visual stimuli are more active when attention needs to be spatially reoriented (invalid cueing) than when attention remains at the cued location (valid cueing), and that partially overlapping specific visual sub-regions mediate reorienting after orienting of endogenous or exogenous attention. Both the present and the TPJ studies provide a comprehensive investigation of endogenous and exogenous attention, and pave the way for rigorous psychophysics informed, neuroimaging studies of covert, spatial attention. Here, we concentrated the analysis on visual cortical areas in the occipital lobe because the slice prescription covered only a limited portion of the brain. The present findings further our knowledge of the neurophysiological bases of covert attention and have implications for models of visual attention, which should consider not only the similarities, but also the differences in the orienting and reorienting of endogenous and exogenous attention in occipital areas reported here.

CONCLUSION

The present results show some similarities and reveal important differences in the specific neural correlates of endogenous and exogenous attention on early vision: An increasing modulation of fMRI activity for pre-cueing endogenous attention, but constant modulation for exogenous attention, along the hierarchy of visual occipital areas, as well as a reliable and constant modulation of fMRI activity for post-cueing endogenous attention in occipital areas but not for exogenous attention. These results suggest that endogenous attention facilitates both the encoding and the readout of visual information whereas exogenous attention only facilitates the encoding of information.

431 **MATERIALS and METHODS**

432 The behavioral methods employed in this study and the behavioral results are the same
433 as those we reported in a recent study, in which we compared activity in TPJ during orienting and
434 reorienting of endogenous and exogenous attention [39]. To maximize the effects of these two
435 types of attention, i.e. the benefits at the attended location and concurrent costs at the unattended
436 location, we used optimal spatial and temporal parameters (reviews by [1,2]). To enable direct com-
437 parison between endogenous and exogenous attention, the same participants performed the
438 same orientation discrimination task under both types of attention. The fMRI methods employed
439 in this study are the same as those used in that study [39], but here, instead of analyzing TPJ
440 activity, we analyzed activity in occipital areas.

441 **Participants**

442 Five participants (two male and three female, 24-30 years-old) participated in the study.
443 They all had normal or corrected-to-normal vision. The University Committee on
444 Activities Involving Human Subjects at New York University approved the experimental protocol
445 (IRB # 10-7094), and participants provided written informed consent. Our study used single-
446 participant ROI-based analysis, and thus had a small sample size. The same sample size that
447 has been used in many fMRI studies in our labs (e.g. [23,25,39,74,99,117-120]), as well as in other labs
448 (e.g. [121-125]). Each participant performed nine scanning sessions: one session to obtain a set of
449 three high-resolution anatomical volumes, two sessions for retinotopic mapping, three sessions
450 for the exogenous attention condition and three sessions for the endogenous attention condition
451 (with the order counterbalanced among participants). Participants performed several practice
452 sessions outside the scanner prior to the first scanning session of each attention condition.

453 **Stimuli**

454 Stimuli were generated on a Macintosh computer using the MGL toolbox [126] in MATLAB
455 (MathWorks). Stimuli were presented on a flat-panel display (NEC, LC-XG250 MultiSync LCD
456 2110; refresh rate: 60 Hz; resolution: 1024 x 768 pixels) positioned at the rear of the scanner
457 bore and housed in a Faraday box with an electrically conductive glass front. The display,

458 calibrated and gamma corrected using a linearized lookup table, was at a viewing distance of
459 172 cm from the participant, and visible through an angled mirror attached to the head coil. A
460 central, white fixation cross (0.3°) was presented throughout the experiment. The two stimuli were
461 two 4-cpd gratings windowed by raised cosines (3° of diameter; 7% contrast), one in each bottom
462 quadrant (5° horizontal eccentricity; –2.65° altitude). Both endogenous cues and exogenous cues
463 were white rectangles (0.7°). The endogenous cues appeared adjacent to the fixation cross indi-
464 cating one of the two lower quadrants (0.35° horizontal eccentricity from the edge of the fixation
465 cross, and 0.35° altitude). The exogenous cues appeared adjacent to an upcoming grating stim-
466 ulus, vertically aligned with the stimulus and above the horizontal meridian (1° away from the
467 edge of the grating stimulus; and the edge of the cue 4.44° horizontal eccentricity from the edge
468 of the fixation cross).

469 **Behavioral procedure**

470 An exogenous attention condition trial lasted 1700 ms, whereas an endogenous attention
471 condition trial lasted 1900 ms, the only difference being the stimulus-onset asynchronies (SOA)
472 between the cue and the display; the timing of all the visual stimuli was the same in both attention
473 conditions (**Figure 1**; the display is not at scale for illustration purposes). In the pre-cue condition
474 (40% of the trials), a cue preceded the two gratings. In 40% the post-cue condition, the cue
475 followed the presentation of the gratings. In 'cue-only' trials (10% of the trials), the gratings were
476 not presented. In 'blank' trials (10% of the trials), neither a cue nor the gratings were presented.
477 These trials were then included in the GLM analysis to model the contribution of the visual signal
478 produced by the cue (see MRI procedure). For both pre-cue and post-cue trials, participants were
479 asked to press one of two keys to report the orientation of a target grating, i.e., clockwise or
480 counter-clockwise compared to vertical. Participants pressed a third key in the case of cue-only
481 and blank trials.

482 In both exogenous and endogenous condition, cues were presented for 67 ms, indicating
483 either the bottom left or right quadrant of the screen. The inter-stimulus interval (ISI) between the
484 cue and the grating stimuli was 50 ms for exogenous and 250 ms for endogenous conditions,
485 resulting in SOA of 117 ms and 317 ms. We used the same timings for pre- and post-cue

conditions (e.g. [23,63,74,127]). These delays are optimal to manipulate exogenous and endogenous attention, while keeping the trial duration as similar as possible, and have been shown to maximize the behavioral consequences of each attention condition [44,128-130].

The behavioral effects of endogenous attention are sustained (e.g. [102]) and thus, as shown in ERP studies (e.g. [131]), are still present in later brain activity. Additionally, during 300 ms following cue onset, the brain responses elicited by exogenous and endogenous cues differ (for review [1]). The two grating stimuli were then displayed for 50 ms. For the postcue trials we kept the timings of cue and stimuli constant but inverted the order of their presentation (e.g. [23,63,74,127]). A response cue, presented for 800 ms at the end of the trial after both the cue and the stimuli had disappeared, indicated which one of the two gratings was the target (50% of the trials on the right and the remaining 50% and on the left). The maximum delay between the offset of the grating stimuli and the onset of the response cue was shorter (~400 ms max in the endogenous condition) than typically associated with a demand for working memory (>600 ms; [132]). Immediately following each trial, a change of color of the fixation cross provided visual feedback to the participants, i.e. green for correct or red for incorrect responses. The fixation cross did not change color if participants had missed the response window, i.e. if they had not pressed any key after 530 ms.

In the exogenous attention condition, a peripheral cue was presented, which was not informative regarding the target location or orientation. When the cue location matched the target location, it was considered a valid trial (50% of the trials), otherwise it was considered an invalid trial (the remaining 50% of the trials). In the endogenous attention condition, a central cue pointed to either the left or right quadrant. The cue was informative of the target location but not its orientation (75% valid trials and 25% invalid trials). Participants were informed of this validity. It is important to note that: (1) cue validity does not affect cueing effectiveness for exogenous attention, although it does so do endogenous attention (e.g. [3,133,134]); (2) the short timing and non-informative cue in the exogenous condition ensured that no voluntary component could be involved in the exogenous attentional effect.

513 Endogenous and exogenous attention conditions were performed in separate sessions to
514 ensure optimal manipulation of each attention system. Participants first performed two practice
515 sessions outside the scanner before the first session of each attentional scanning condition. To
516 equate task difficulty for both attention conditions, using a staircase procedure, the tilt of the
517 target grating was adjusted for each participant to achieve ~80% correct performance in the valid
518 trials in each attention condition. In each of the six experimental scanning sessions (three ses-
519 sions of exogenous attention and three of endogenous), participants performed 14 runs of 40
520 trials each, as well as a run of stimulus localizer (see MRI procedure). The tilt was then adjusted
521 between runs to maintain overall performance at ~80% correct.

522 Eye position was monitored during all scanning sessions using an infrared video camera
523 system (Eyelink 1K, SR Research, Ottawa, Ontario, http://www.sr-research.com/EL_1000.html).
524 Trials in which the participants blinked or broke fixation (1.5° radius from central fixation) at any
525 point from fixation onset to response cue offset were identified and regressed separately in the
526 MRI analysis, and removed from the behavioral analysis (13% ± 4% of the trials on average
527 across all participants).

528 **MRI Procedure**

529 *Scanning*

530 Imaging was conducted on a 3T Siemens Allegra head-only scanner (Erlangen, Germany),
531 using a Siemens NM-011 head coil (to transmit and receive) to acquire anatomical images, a
532 receive-only 8-channel surface coil array (Nova Medical, Wilmington, MA) to acquire functional
533 images. To minimize participants' head movements, padding was used.

534 For each participant, three high-resolution anatomic images were acquired in one scanning
535 session, using a T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) sequence
536 (FOV = 256 x 256 mm; 176 sagittal slices; 1 x 1 x 1 mm voxels), and were co-registered and
537 averaged. Using FreeSurfer (public domain software; http://surfer.nmr.mgh.harvard.edu), the
538 gray matter was segmented from these averaged anatomical volumes. All subsequent analyses
539 were constrained only to voxels that intersected gray matter.

540 T2*-weighted echo-planar imaging sequence (i.e. functional images; TR = 1750 ms; TE =
541 30 ms; flip angle = 90°) measured blood oxygen level-dependent (BOLD) changes in image in-
542 tensity [135]. In each volume, 28 slices covered the occipital and posterior parietal lobes and were
543 oriented 45° to the calcarine sulcus (FOV = 192 x 192 mm; resolution = 2 x 2 x 2.5 mm; no gap).
544 To align functional images from different sessions to the same high-resolution anatomical volume
545 for each participant, we acquired an additional T1-weighted anatomical images in the same slices
546 as the functional images (spin echo; TR = 600 ms; TE = 9.1 ms; flip angle = 90°; resolution = 1.5
547 × 1.5 × 3 mm) during each scanning session, and used them in a robust image registration algo-
548 rithm.

549 *MRI data pre-processing*

550 Imaging data were analyzed in MATLAB, using mrTools [136] and custom software. To allow
551 longitudinal magnetization to reach steady state, the first eight volumes of each run were dis-
552 carded. Spatial distortion was corrected using the B0 static magnetic field measurements per-
553 formed in each session. The functional data were then motion corrected, the linear trend was
554 removed, and a temporal high-pass filter was applied (cutoff: 0.01 Hz) to remove slow drifts and
555 low-frequency noise in the fMRI signal.

556 *Retinotopic mapping*

557 We followed well-established conventional traveling-wave, phase-encoded methods. Using
558 clockwise and counter-clockwise rotating checkerboard wedges, we measured phase maps of
559 polar angle. Using contracting and expending checkerboard rings, we measured eccentricity
560 maps [93-96]. **Figure 2** (left panel) shows the visual areas that were drawn by hand on flattened
561 surface of the brain, following published conventions [95,96,99,137].

562 *Stimulus localizer*

563 In each scanning session of the main experiment, participants completed one stimulus lo-
564 calizer run (6 runs overall, 4 min each). A run consisted of 16 cycles (17.5 s) of a block alternation
565 protocol between stimulus on (8.75 s) and stimulus off (8.75 s). Participants only had to fixate the
566 central cross throughout each run. The stimuli were at the same location, and of the same size

and spatial frequency as those in the main experiment, except at full contrast and their phase and orientation changed randomly every 200 ms to avoid adaptation. To define the cortical representation of the gratings, we then averaged the data across the 6 runs and followed the same methods as for the retinotopic mapping. Voxels that responded positively during the blocks when the grating stimuli were presented were used to restrict each retinotopic ROI. The fMRI time series from each voxel were fit to a sinusoid. To be conservative, only voxels whose best-fit sinusoid had a phase value between 0 and pi, and a coherence between the best-fit sinusoid and the time series greater than 0.2 were included in the ROI (**Figure 2**, right panel). Analysis performed without restricting the ROI to this coherence level yielded similar results.

Event-related analysis

fMRI time series were averaged across voxels in each ROI (separately for each hemisphere) and then concatenated across runs. The data were denoised using GLMDenoise [138], and fMRI response amplitudes were computed using linear regression, with twelve regressors: 8 combinations of right and left valid and invalid pre- and post-cue, right and left cue-only, blank (no cue nor stimulus) and eye-movements (blink or broken fixation). For each ROI in each hemisphere, the resulting fMRI response amplitudes (for correct trials only) were then averaged across participants.

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Data availability: Data relative to the main results of this study (i.e. Figures 4, 5 and 6) are made available via OSF at [link provided upon acceptance of the manuscript].

REFERENCES

1. Carrasco, M. Visual attention: the past 25 years. *Vision Res.* **51,** 1484–1525 (2011).
2. Carrasco, M. & Barbot, A. How attention affects spatial resolution. *Cold Spring Harbor Symposia on Quantitative Biology* (2015).
3. Giordano, A. M., McElree, B. & Carrasco, M. On the automaticity and flexibility of covert attention: a speed-accuracy trade-off analysis. *Journal of Vision* **9,** 30.1–10 (2009).
4. Pestilli, F., Ling, S. & Carrasco, M. A population-coding model of attention's influence on contrast response: Estimating neural effects from psychophysical data. *Vision Res.* **49,** 1144–1153 (2009).
5. Ling, S. & Carrasco, M. Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Res.* **46,** 1210–1220 (2006).
6. Dosher, B. A. & Lu, Z. L. Mechanisms of perceptual attention in precuing of location. *Vision Res.* **40,** 1269–1292 (2000).
7. Barbot, A., Landy, M. S. & Carrasco, M. Differential effects of exogenous and endogenous attention on second-order texture contrast sensitivity. *Journal of Vision* **12,** 6–6 (2012).
8. Yeshurun, Y. & Carrasco, M. Attention improves or impairs visual performance by enhancing spatial resolution. *Nature* **396,** 72–75 (1998).
9. Carrasco, M., Giordano, A. M. & McElree, B. Attention speeds processing across eccentricity: Feature and conjunction searches. *Vision Res.* **46,** 2028–2040 (2006).
10. Yeshurun, Y., Montagna, B. & Carrasco, M. On the flexibility of sustained attention and its effects on a texture segmentation task. *Vision Res.* **48,** 80–95 (2008).
11. Barbot, A. & Carrasco, M. Attention Modifies Spatial Resolution According to Task Demands. *Psychological Science* **28,** 285–296 (2017).
12. Jigo, M. & Carrasco, M. Attention alters spatial resolution by modulating second-order processing. *Journal of Vision* **18,** 2 (2018).
13. Anton-Erxleben, K. & Carrasco, M. Attentional enhancement of spatial resolution: linking behavioural and neurophysiological evidence. *Nat. Rev. Neurosci.* **14,** 188–200 (2013).
14. Carrasco, M. & Yeshurun, Y. Covert attention effects on spatial resolution. *Prog. Brain Res.* **176,** 65–86 (2009).
15. Reynolds, J. H. & Heeger, D. J. The Normalization Model of Attention. *Neuron* **61,** 168–185 (2009).
16. Martínez-Trujillo, J. C. & Treue, S. Attentional Modulation Strength in Cortical Area MT Depends on Stimulus Contrast. *Neuron* **35,** 365–370 (2002).
17. McAdams, C. J. & Maunsell, J. H. R. Effects of Attention on Orientation-Tuning Functions of Single Neurons in Macaque Cortical Area V4. *J. Neurosci.* **19,** 431–441 (1999).
18. Mitchell, J. F., Sundberg, K. A. & Reynolds, J. H. Spatial Attention Decorrelates Intrinsic Activity Fluctuations in Macaque Area V4. *Neuron* **63,** 879–888 (2009).
19. Reynolds, J. H., Pasternak, T. & Desimone, R. Attention increases sensitivity of V4 neurons. *Neuron* **26,** 703–714 (2000).
20. Williford, T. & Maunsell, J. H. R. Effects of Spatial Attention on Contrast Response Functions in Macaque Area V4. *J. Neurophysiol.* **96,** 40–54 (2006).
21. Luo, T. Z. & Maunsell, J. H. R. Neuronal Modulations in Visual Cortex Are Associated with Only One of Multiple Components of Attention. *Neuron* **86,** 1182–1188 (2015).
22. Ruff, D. A. & Cohen, M. R. Attention can either increase or decrease spike count correlations in visual cortex. *Nat. Neurosci.* **17,** 1591–1597 (2014).
23. Pestilli, F., Carrasco, M., Heeger, D. J. & Gardner, J. L. Attentional enhancement via selection and pooling of early sensory responses in human visual cortex. *Neuron* **72,** 832–846 (2011).
24. Murray, S. O. The effects of spatial attention in early human visual cortex are stimulus independent. *Journal of Vision* **8,** 2.1–11 (2008).
25. Herrmann, K., Montaser-Kouhsari, L., Carrasco, M. & Heeger, D. J. When size matters: attention affects performance by contrast or response gain. *Nat. Neurosci.* **13,** 1554–1559 (2010).

26. Buracas, G. T. & Boynton, G. M. The effect of spatial attention on contrast response functions in human visual cortex. *Journal of Neuroscience* **27,** 93–97 (2007).
27. O'Connor, D. H., Fukui, M. M. & Pinsk, M. A. Attention modulates responses in the human lateral geniculate nucleus - ProQuest. *Nature* **5,** 1203–1209 (2002).
28. Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R. & Ungerleider, L. G. Increased Activity in Human Visual Cortex during Directed Attention in the Absence of Visual Stimulation. *Neuron* **22,** 751–761 (1999).
29. Somers, D. C., Dale, A. M., Seiffert, A. E. & Tootell, R. B. Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *PNAS* **96,** 1663–1668 (1999).
30. Beck, D. M. & Kastner, S. Neural systems for spatial **attention** in the human brain: Evidence from neuroimaging in the framework of biased competition. *The Oxford Handbook of Attention* 253–288 (2014).
31. Lu, Z.-L., Li, X., Tjan, B. S., Dosher, B. A. & Chu, W. Attention Extracts Signal in External Noise: A BOLD fMRI Study. *J Cogn Neurosci* **23,** 1148–1159 (2011).
32. Li, X., Lu, Z.-L., Tjan, B. S., Dosher, B. A. & Chu, W. Blood oxygenation level-dependent contrast response functions identify mechanisms of covert attention in early visual areas. *Proc. Natl. Acad. Sci. U.S.A.* **105,** 6202–6207 (2008).
33. Busse, L., Katzner, S. & Treue, S. Temporal dynamics of neuronal modulation during exogenous and endogenous shifts of visual attention in macaque area MT. *Proc. Natl. Acad. Sci. U.S.A.* **105,** 16380–16385 (2008).
34. Wang, F., Chen, M., Yan, Y., Zhaoping, L. & Li, W. Modulation of Neuronal Responses by Exogenous Attention in Macaque Primary Visual Cortex. *Journal of Neuroscience* **35,** 13419–13429 (2015).
35. Corbetta, M. & Shulman, G. L. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* **3,** 201–215 (2002).
36. Chica, A. B., Bartolomeo, P. & Lupiáñez, J. Two cognitive and neural systems for endogenous and exogenous spatial attention. *Behavioural Brain Research* **237,** 107–123 (2013).
37. Bowling, J. T., Friston, K. J. & Hopfinger, J. B. Top-down versus bottom-up attention differentially modulate frontal–parietal connectivity. *Hum Brain Mapp* **9,** 1116 (2019).
38. Hahn, B., Ross, T. J. & Stein, E. A. Neuroanatomical dissociation between bottom–up and top–down processes of visuospatial selective attention. *Neuroimage* **32,** 842–853 (2006).
39. Dugué, L., Merriam, E. P., Heeger, D. J. & Carrasco, M. Specific Visual Subregions of TPJ Mediate Reorienting of Spatial Attention. *Cereb. Cortex* 1–16 (2017). doi:10.1093/cercor/bhx140
40. Geng, J. J. & Vossel, S. Re-evaluating the role of TPJ in attentional control: contextual updating? *Neurosci Biobehav Rev* **37,** 2608–2620 (2013).
41. Doricchi, F., Macci, E., Silvetti, M. & Macaluso, E. Neural correlates of the spatial and expectancy components of endogenous and stimulus-driven orienting of attention in the Posner task. *Cereb. Cortex* **20,** 1574–1585 (2010).
42. Silvetti, M. *et al.* The Response of the Left Ventral Attentional System to Invalid Targets and its Implication for the Spatial Neglect Syndrome: a Multivariate fMRI Investigation. *Cereb. Cortex* 1–12 (2015). doi:10.1093/cercor/bhv208
43. Beck, D. M. & Kastner, S. Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Res.* **49,** 1154–1165 (2009).
44. Nakayama, K. & Mackeben, M. Sustained and transient components of focal visual attention. *Vision Res.* **29,** 1631–1647 (1989).
45. Posner, M. I., Snyder, C. R. & Davidson, B. J. Attention and the detection of signals. *J Exp Psychol* **109,** 160–174 (1980).
46. Buschman, T. J. & Miller, E. K. Serial, Covert Shifts of Attention during Visual Search Are Reflected by the Frontal Eye Fields and Correlated with Population Oscillations. *Neuron* **63,** 386–396 (2009).
47. Corbetta, M., Patel, G. & Shulman, G. L. The reorienting system of the human brain: from environment to theory of mind. *Neuron* **58,** 306–324 (2008).

48. Peelen, M. V., Heslenfeld, D. J. & Theeuwes, J. Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *Neuroimage* **22,** 822–830 (2004).
49. Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L. & Corbetta, M. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *Journal of Neuroscience* **25,** 4593–4604 (2005).
50. Mayer, A. R., Dorflinger, J. M., Rao, S. M. & Seidenberg, M. Neural networks underlying endogenous and exogenous visual–spatial orienting. *Neuroimage* **23,** 534–541 (2004).
51. Carrasco, M. & McElree, B. Covert attention accelerates the rate of visual information processing. *PNAS* **98,** 5363–5367 (2001).
52. Reed, A. V. Speed-Accuracy Trade-Off in Recognition Memory. *Science* **181,** 574–576 (1973).
53. Wickelgren, W. A. Speed-accuracy tradeoff and information processing dynamics. *Acta Psychologica* **41,** 67–85 (1977).
54. Correa, Á., Triviño, M., Pérez-Dueñas, C., Acosta, A. & Lupiáñez, J. Temporal preparation, response inhibition and impulsivity. *Brain and Cognition* **73,** 222–228 (2010).
55. Yashar, A. & Lamy, D. Refining the dual-stage account of intertrial feature priming: does motor response or response feature matter? *Atten Percept Psychophys* **73,** 2160–2167 (2011).
56. Herath, P., Klingberg, T., Young, J., Amunts, K. & Roland, P. E. Neural Correlates of Dual Task Interference Can be Dissociated from Those of Divided Attention: an fMRI Study | Cerebral Cortex | Oxford Academic. *Cereb. Cortex* **11,** 796–805 (2001).
57. Culham, J. C., Cavanagh, P. & Kanwisher, N. G. Attention Response Functions: Characterizing Brain Areas Using fMRI Activation during Parametric Variations of Attentional Load. *Neuron* **32,** 737–745 (2001).
58. Beauchamp, M. S., Petit, L., Ellmore, T. M., Ingeholm, J. & Haxby, J. V. A parametric fMRI study of overt and covert shifts of visuospatial attention. *Neuroimage* **14,** 310–321 (2001).
59. Carrasco, M., Evert, D. L., Chang, I. & Katz, S. M. The eccentricity effect: target eccentricity affects performance on conjunction searches. *Perception & Psychophysics* **57,** 1241–1261 (1995).
60. Rosen, A. C. *et al.* Neural basis of endogenous and exogenous spatial orienting. A functional MRI study. *Journal of Cognitive Neuroscience* **11,** 135–152 (1999).
61. Esterman, M. *et al.* Voluntary and involuntary attention affect face discrimination differently. *Neuropsychologia* **46,** 1032–1040 (2008).
62. Natale, E., Marzi, C. A., Girelli, M., Pavone, E. F. & Pollmann, S. ERP and fMRI correlates of endogenous and exogenous focusing of visual-spatial attention. *Eur. J. Neurosci.* **23,** 2511–2521 (2006).
63. Kinchla, R. A., Chen, Z. & Evert, D. Precue effects in visual search: data or resource limited? *Perception & Psychophysics* **57,** 441–450 (1995).
64. Ruff, C. C., Kristjánsson, Á. & Driver, J. Readout from iconic memory and selective spatial attention involve similar neural processes. *Psychological Science* **18,** 901–909 (2007).
65. Hulme, O. J., Friston, K. F. & Zeki, S. Neural correlates of stimulus reportability. *Journal of Cognitive Neuroscience* **21,** 1602–1610 (2009).
66. Nobre, A. C. *et al.* Orienting attention to locations in perceptual versus mental representations. *Journal of Cognitive Neuroscience* **16,** 363–373 (2004).
67. Sergent, C., Ruff, C. C., Barbot, A., Driver, J. & Rees, G. Top-down modulation of human early visual cortex after stimulus offset supports successful postcued report. *Journal of Cognitive Neuroscience* **23,** 1921–1934 (2011).
68. Thibault, L., van den Berg, R., Cavanagh, P. & Sergent, C. Retrospective Attention Gates Discrete Conscious Access to Past Sensory Stimuli. *PLoS ONE* **11,** e0148504 (2016).
69. Sergent, C. *et al.* Cueing Attention after the Stimulus Is Gone Can Retrospectively Trigger Conscious Perception. *Current Biology* **23,** 150–155 (2013).
70. Gobell, J. & Carrasco, M. Attention alters the appearance of spatial frequency and gap size. *Psychological Science* **16,** 644–651 (2005).

71. Anton-Erxleben, K., Henrich, C. & Treue, S. Attention changes perceived size of moving visual patterns. *Journal of Vision* **7,** 5.1–9 (2007).
72. Fuller, S., Park, Y. & Carrasco, M. Cue contrast modulates the effects of exogenous attention on appearance. *Vision Res.* **49,** 1825–1837 (2009).
73. Carrasco, M. & Yeshurun, Y. The contribution of covert attention to the set-size and eccentricity effects in visual search. *Journal of Experimental Psychology: Human Perception and Performance* **24,** 673–692 (1998).
74. Liu, T., Pestilli, F. & Carrasco, M. Transient attention enhances perceptual performance and FMRI response in human visual cortex. *Neuron* **45,** 469–477 (2005).
75. Kim, Y. H. *et al.* The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *Neuroimage* **9,** 269–277 (1999).
76. Meyer, K. N., Du, F., Parks, E. & Hopfinger, J. B. Exogenous vs. endogenous attention: Shifting the balance of fronto-parietal activity. *Neuropsychologia* **111,** 307–316 (2018).
77. Dugué, L., Roberts, M. & Carrasco, M. Attention Reorients Periodically. *Current Biology* **26,** 1595–1601 (2016).
78. Senoussi, M., Moreland, J. C., Busch, N. A. & Dugué, L. Attention explores space periodically at the theta frequency. *Journal of Vision* **19,** 22–22 (2019).
79. Maunsell, J. H. R. & Cook, E. P. The role of attention in visual processing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **357,** 1063–1072 (2002).
80. Kastner, S. & Pinsk, M. A. Visual attention as a multilevel selection process. *Cognitive, Affective, & Behavioral Neuroscience* **4,** 483–500 (2004).
81. Klein, B. P., Harvey, B. M. & Dumoulin, S. O. Attraction of Position Preference by Spatial Attention throughout Human Visual Cortex. *Neuron* **84,** 227–237 (2014).
82. Kay, K. N., Weiner, K. S. & Grill-Spector, K. Attention Reduces Spatial Uncertainty in Human Ventral Temporal Cortex. *Current Biology* **25,** 595–600 (2015).
83. Nachmias, J. Effect of Exposure Duration on Visual Contrast Sensitivity with Square-Wave Gratings. *J. Opt. Soc. Am., JOSA* **57,** 421–427 (1967).
84. Carrasco, M., Penpeci-Talgar, C. & Eckstein, M. Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Res.* **40,** 1203–1215 (2000).
85. Luck, S. J. *et al.* Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception and Performance* **20,** 887–904 (1994).
86. Lu, Z. L. & Dosher, B. A. External noise distinguishes attention mechanisms. *Vision Res.* **38,** 1183–1198 (1998).
87. Pestilli, F. & Carrasco, M. Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Res.* **45,** 1867–1875 (2005).
88. Montagna, B., Pestilli, F. & Carrasco, M. Attention trades off spatial acuity. *Vision Res.* **49,** 735–745 (2009).
89. Yeshurun, Y. & Rashal, E. Precueing attention to the target location diminishes crowding and reduces the critical distance. *Journal of Vision* **10,** 16–16 (2010).
90. Senoussi, M., Moreland, J. C., Busch, N. A. & Dugué, L. **Attention explores space periodically at the theta frequency**. *Journal of Vision* **19,** 1–17 (2019).
91. Dugué, L., Xue, A. M. & Carrasco, M. Distinct perceptual rhythms for feature and conjunction searches. *Journal of Vision* **17,** 22–22 (2017).
92. Ling, S. & Carrasco, M. Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Res.* **46,** 1210–1220 (2006).
93. Engel, S. A. *et al.* fMRI of human visual cortex. *Nature* **369,** 525 (1994).
94. Sereno, M. I. *et al.* Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* **268,** 889–893 (1995).
95. Engel, S. A., Glover, G. H. & Wandell, B. A. Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb. Cortex* **7,** 181–192 (1997).
96. Larsson, J. & Heeger, D. J. Two retinotopic visual areas in human lateral occipital cortex. *Journal of Neuroscience* **26,** 13128–13142 (2006).

97. Ress, D., Backus, B. T. & Heeger, D. J. Activity in primary visual cortex predicts performance in a visual detection task. *Nat. Neurosci.* **3,** 940–945 (2000).
98. Giesbrecht, B., Weissman, D. H., Woldorff, M. G. & Mangun, G. R. Pre-target activity in visual cortex predicts behavioral performance on spatial and feature attention tasks. *Brain Res.* **1080,** 63–72 (2006).
99. Liu, T., Larsson, J. & Carrasco, M. Feature-based attention modulates orientation-selective responses in human visual cortex. *Neuron* **55,** 313–323 (2007).
100. Pinheiro, J. C. & Bates, D. M. Unconstrained parametrizations for variance-covariance matrices. *Stat Comput* **6,** 289–296 (1996).
101. Carrasco, M., Marie Giordano, A. & McElree, B. Temporal performance fields: visual and attentional factors. *Vision Res.* **44,** 1351–1365 (2004).
102. Ling, S. & Carrasco, M. When sustained attention impairs perception. *Nat. Neurosci.* **9,** 1243–1245 (2006).
103. Liu, T., Abrams, J. & Carrasco, M. Voluntary attention enhances contrast appearance. *Psychological Science* **20,** 354–362 (2009).
104. Harvey, B. M. & Dumoulin, S. O. The relationship between cortical magnification factor and population receptive field size in human visual cortex: constancies in cortical architecture. *Journal of Neuroscience* **31,** 13604–13612 (2011).
105. Harvey, B. M. & Dumoulin, S. O. Visual motion transforms visual space representations similarly throughout the human visual hierarchy. *Neuroimage* **127,** 173–185 (2016).
106. Michalareas, G. *et al.* Alpha-Beta and Gamma Rhythms Subserve Feedback and Feedforward Influences among Human Visual Cortical Areas. *Neuron* **89,** 384–397 (2016).
107. Yildirim, F., Carvalho, J. & Cornelissen, F. W. A second-order orientation-contrast stimulus for population-receptive-field-based retinotopic mapping. *Neuroimage* **164,** 183–193 (2018).
108. Fritsche, M., Lawrence, S. J. D. & de Lange, F. P. Temporal tuning of repetition suppression across the visual cortex. *J. Neurophysiol.* **123,** 224–233 (2020).
109. Boynton, G. M., Demb, J. B., Glover, G. H. & Heeger, D. J. Neuronal basis of contrast discrimination. *Vision Res.* **39,** 257–269 (1999).
110. Brefczynski, J. A. & DeYoe, E. A. A physiological correlate of the 'spotlight' of visual attention. *Nat. Neurosci.* **2,** 370–374 (1999).
111. Müller, N. G. & Kleinschmidt, A. Temporal Dynamics of the Attentional Spotlight: Neuronal Correlates of Attentional Capture and Inhibition of Return in Early Visual Cortex. *J Cogn Neurosci* **19,** 587–593 (2007).
112. Müller, N. G. & Ebeling, D. Attention-modulated activity in visual cortex—More than a simple 'spotlight'. *Neuroimage* **40,** 818–827 (2008).
113. Heinen, K. *et al.* Concurrent TMS-fMRI reveals dynamic interhemispheric influences of the right parietal cortex during exogenously cued visuospatial attention. *European Journal of Neuroscience* **33,** 991–1000 (2011).
114. Mulckhuyse, M., Belopolsky, A. V., Heslenfeld, D., Talsma, D. & Theeuwes, J. Distribution of attention modulates salience signals in early visual cortex. *PLoS ONE* **6,** e20379 (2011).
115. Kay, K. N., Winawer, J., Rokem, A., Mezer, A. & Wandell, B. A. A two-stage cascade model of BOLD responses in human visual cortex. *PLoS Comput. Biol.* **9,** e1003079 (2013).
116. Chica, A. B. & Lupiáñez, J. Effects of endogenous and exogenous attention on visual processing: an Inhibition of Return study. *Brain Res.* **1278,** 75–85 (2009).
117. Liu, T., Heeger, D. J. & Carrasco, M. Neural correlates of the visual vertical meridian asymmetry. *Journal of Vision* **6,** 1294–1306 (2006).
118. Freeman, J., Heeger, D. J. & Merriam, E. P. Coarse-scale biases for spirals and orientation in human visual cortex. *Journal of Neuroscience* **33,** 19695–19703 (2013).
119. Wang, H. X., Merriam, E. P., Freeman, J. & Heeger, D. J. Motion direction biases and decoding in human visual cortex. *Journal of Neuroscience* **34,** 12601–12615 (2014).
120. Brouwer, G. J., Arnedo, V., Offen, S., Heeger, D. J. & Grant, A. C. Normalization in human somatosensory cortex. *J. Neurophysiol.* **114,** 2588–2599 (2015).

121. McMains, S. A. & Somers, D. C. Multiple spotlights of attentional selection in human visual cortex. *Neuron* **42,** 677–686 (2004).
122. Bloem, I. M. & Ling, S. Normalization governs attentional modulation within human visual cortex. *Nature Communications* **10,** 5660–10 (2019).
123. Poltoratski, S., Ling, S., McCormack, D. & Tong, F. Characterizing the effects of feature salience and top-down attention in the early visual system. *J. Neurophysiol.* **118,** 564–573 (2017).
124. Moerel, D., Ling, S. & Jehee, J. F. M. Perceptual learning increases orientation sampling efficiency. *Journal of Vision* **16,** 36–36 (2016).
125. Mackey, W. E., Winawer, J. & Curtis, C. E. Visual field map clusters in human frontoparietal cortex. *Elife* **6,** 2704 (2017).
126. Gardner, J. L., Merriam, E. P., Schluppeck, D. & Larsson, J. MGL: Visual psychophysics stimuli and experimental design package. (2018). doi:10.5281/zenodo.1299497
127. Yaffa Yeshurun, M. C. Attention improves or impairs visual performance by enhancing spatial resolution. *Nature* **396,** 72–75 (1998).
128. Müller, M. M. in *Cognitive Electrophysiology of Attention* 123–135 (Elsevier, 2014). doi:10.1016/B978-0-12-398451-7.00010-5
129. Mackeben, M. & Nakayama, K. Express attentional shifts. *Vision Res.* **33,** 85–90 (1993).
130. Liu, T., Stevens, S. T. & Carrasco, M. Comparing the time course and efficacy of spatial and feature-based attention. *Vision Res.* **47,** 108–113 (2007).
131. Seiss, E., Driver, J. & Eimer, M. Effects of attentional filtering demands on preparatory ERPs elicited in a spatial cueing task. *Clin Neurophysiol* **120,** 1087–1095 (2009).
132. Phillips, W. A. On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics* **16,** 283–290 (1974).
133. Sperling, G. & Melchner, M. J. The attention operating characteristic: examples from visual search. *Science* **202,** 315–318 (1978).
134. Kinchla, R. A. The measurement of attention. *Attention and performance VIII* 213–238 (1980).
135. Ogawa, S., Lee, T. M., Kay, A. R. & Tank, D. W. Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proc. Natl. Acad. Sci. U.S.A.* **87,** 9868–9872 (1990).
136. Gardner, J. L., Merriam, E. P., Schluppeck, D., Besle, J. & Heeger, D. J. mrTools: Analysis and visualization package for functional magnetic resonance imaging data. (2018). doi:10.5281/zenodo.1299483
137. Wandell, B. A., Dumoulin, S. O. & Brewer, A. A. Visual field maps in human cortex. *Neuron* **56,** 366–383 (2007).
138. Kay, K., Rokem, A., Winawer, J., Dougherty, R. & Wandell, B. GLMdenoise: a fast, automated technique for denoising task-based fMRI data. *Front. Neurosci.* **7,** 1–15 (2013).