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

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ABSTRACT (150 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 orientation 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 was 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 reviews 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. [4-9]); 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, it hampers performance where resolution is already high for the task at hand (e.g. [10-15]).

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 [1,2,16,17]). Specifically, single-unit studies in monkeys have demonstrated effects of endogenous attention in occipital areas (e.g. [18-25]). Additionally, fMRI studies have shown that endogenous attention causes a baseline shift in early visual areas (e.g. [26-32]; review by [33]) and increases the dynamic range of fMRI responses [34,35]. Comparatively, little is known about the effect of exogenous attention on visual areas both from single-unit studies [36,37] and fMRI studies (for reviews see [1,16]).

Since Corbetta and Schulman's seminal review (2002) [38] 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 [33,39,40]). Yet, there remains considerable debate regarding the dissociation between dorsal regions, for endogenous attention, and

ventral regions, for exogenous attention (e.g. [40,41]), including the role of the temporo-parietal junction (TPJ; [42-45]). Classically, researchers have described endogenous attention as a top-down process, and exogenous attention as a bottom-up process [1,38-40,46-48]. 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 [1,33,39,46]).

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 [40,49]. 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 [33,38,39,50,51].

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 [40,51-53]:

(1) The effect of attention on behavioral performance was assessed in some studies with a detection task using RT as their only dependent variable [51,53], in which performance may differ due to speed of processing, discriminability or criterion [54-56] and/or motor behavior [57,58].

(2) In the studies in which performance was assessed in a discrimination task using RT [52], small RT differences were reported, which could have resulted from speed of processing, discriminability, or criterion factors [54-56].

(3) In the studies in which accuracy was not assessed [40,51,53], 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 [59,60].

(4) For the studies in which eye position was not monitored while participants performed the task in the scanner [40,51-53], the results could be due to covert attention, overt attention or both [1,61,62].

(5) Given that exogenous attention is a fast, transient process (for reviews see [1,2,16,17]), it was inappropriately manipulated in the studies in which long stimulus onset asynchronies (SOA) were used [51,52,63-65] 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) [65] and the other in the TPJ [42], 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 [51-53], 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 [42], 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 [66-69] and modulate fMRI activity in early visual areas [26,68-70]. Exogenous post-cues also affect performance in some tasks [71,72], but not in others [73-76], and the only fMRI study evaluating post-cues in exogenous attention in occipital cortex showed no such modulation [77]. Critically, no single study has compared visual cortex activity with post-cues in endogenous and exogenous attention.

Table 1

Study	Cueing manipulation		Task	Dependent Variable	Analysis	Cortical areas	Eye tracking
	Endogenous	Exogenous					
Studies including Occipital areas							
Detection tasks							
Mayer et al. (2004)[53]	central arrow 70% valid	luminance change of peripheral placeholder; 50% valid	X	RT	Group-averaged	**Occipital:** *Cuneus, MOG, SOG* + Frontal Temporo-Parietal	No
	SOA=100 or 800 ms						
Peelen et al. (2004)[51]	central arrow 75% valid	brightening of peripheral place-holder; 50% valid;	square	RT	Group-averaged	**Occipital:** *Cuneus* + Frontal Temporo-Parietal	No
	SOA=550 ms						
Natale et al. (2006)[64]	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
	SOA=8, 8.15, 8.3, 8.45 or 8.6 s						
Discrimination tasks							
Kincade et al. (2005)[52]	brightening of half of central fixa-tion 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
	SOA=2160 ms						
Esterman et al. (2008)[65]	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
	SOA=300 ms						
Current study	central bar; 75% invalid SOA=310 ms	peripheral bar; 50% valid; SOA=110 ms	orientation	d' (RT)	ROI-based	**Occipital:** *V1, V2, V3, V3A, hV4, LO1*	Yes
Studies NOT including Occipital areas							
Detection tasks							
Rosen et al. (1999)[63]	central arrow; 80% valid;	peripheral dot; 50% valid;	filling of a square	RT	Group-averaged	Frontal Temporo-Parietal	No
	SOA=400, 550 or 700 ms						
Discrimination tasks							
Kim et al. (1999)[78]	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
Meyer et al. (2018)[79]	color change of central fixation 83% valid SOA=700–1000 ms	whitening of peripheral place-holder 50% valid SOA=100–300 ms	central color of a checkerboard	Inverse effi-ciency = RT/%correct	Group-averaged	Frontal Temporo-Parietal	No
Dugué et al. (2017)[42]	central bar; 75% invalid; SOA=310 ms	peripheral bar; 50% valid; SOA=110 ms	orientation	d' (RT)	ROI-based	Temporo-Parietal	Yes
Bowling et al. (2019)[40]	color change of central fixation; 83% valid; SOA=700–1000 ms	whitening of peripheral place-holder; 50% valid; SOA=100–300 ms	central color of a checkerboard	Inverse effi-ciency = RT/%correct	Group-averaged	Frontal Temporo-Parietal	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 statistics or ROI-based on single-participants, the cortical areas reported in the publications and showing significant activation due to cue and/or target, and whether or not eye data were monitored in the scanner or used for the subsequent fMRI analysis. 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 systematically tested the following four predictions: (1) Pre-cueing should induce an attentional modulation of fMRI activity (for reviews see [1,16,33,39,40]), higher in the valid than the invalid condition in which attention needs to be reoriented to the opposite location (e.g. [42,50,80,81]) 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. [26,77]). (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; [26,31]; for reviews [33,39]). 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 [31,32,39,82-85]. (4) Post-cueing endogenous [26,68-70], but not exogenous [77], attention should induce attentional modulation of fMRI activity in early visual areas. Voluntary, endogenous attention would facilitate reading out perceptual information [42], and modulate its processing [26,68-70]. The only fMRI study assessing the effects of post-cueing exogenous attention in occipital cortex found no attentional modulation of fMRI activity [77]; some behavioral studies report post-cueing effects [71,72] but others found no such effects [73-76].

149 To test these four predictions, we measured fMRI activity and compared the effects of
150 endogenous and exogenous attention in early (V1, V2, V3) and intermediate (V3A, hV4, LO1)
151 visual areas while the same participants performed the same task –a two-Alternative Forced
152 Choice (2-AFC) orientation discrimination task, contingent upon contrast sensitivity [4,5,8,80,86-89].
153 We used a fully-crossed design: two attention conditions –endogenous or exogenous attention-
154 al orienting– and two types of cueing –pre- or post-cue. We evaluated fMRI activity at both the
155 attended and the un-attended locations, given the ubiquitous performance tradeoffs at attended
156 (benefits) and unattended (costs) locations compared to a neutral condition (e.g. [3,28,88-93]), and
157 the importance of evaluating both the orienting and reorienting of attention, critical in an ever-
158 changing environment [42,80,81,94].
159 This is the first study to systematically evaluate and directly compare how pre and post-
160 orienting, and reorienting, of endogenous and exogenous attention modulate neural activity in
161 visual cortex to affect behavior. The results indicate that these two types of spatial covert atten-
162 tion distinctly modulate activity in individual retinotopic visual cortical areas. These differences
163 in activity are consonant with differential engagement of top-down and bottom-up processes
164 and their respective temporal dynamics. These results suggest that endogenous attention facili-
165 tates both the encoding and the readout of visual information whereas exogenous attention only
166 facilitates the encoding of information.
167
168 **RESULTS**
169 **Endogenous and exogenous attention improve performance**
170 Participants performed a 2-AFC orientation-discrimination task under two attentional con-
171 ditions (exogenous or endogenous attention), when the cue was presented either before (pre-
172 cue) or after (post-cue) the grating stimuli (see Methods), while their brain activity was meas-
173 ured with fMRI (**Figure 1**).
174 In each condition, we calculated performance accuracy (d'), as the main dependent vari-
175 able, for each participant separately (**Figure 1B**, top row). A three-way repeated measures
176 2x2x2 ANOVA (exogenous/endogenous x valid/invalid x pre/post-cue) revealed higher perfor-

mance for valid than invalid cues ($F(1,4)=23.6$, $p=0.008$), that the effect of exogenous and endogenous cues were statistically indistinguishable ($F(1,4)<1$), and that there was no significant difference between pre- and post-cues ($F(1,4)<1$). None of the two and three-way interactions were significant ($F<1$).

In each condition, we also calculated reaction time (RT), as a secondary dependent variable for each participant separately (**Figure 1B**, bottom row). Although the task is not optimal to asse RT effects due to the long response cue window during which participants are not allowed to provide their response, we assessed RT to rule out speed-accuracy tradeoffs. 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 [3-6,8,28,80,87-89,91], 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. [95-98]).

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 –

204 and each cueing condition – pre- and post-cueing, for the contralateral and ipsilateral side to
205 the cued (attended) location. We analyzed the fMRI responses evoked by each type of atten-
206 tion in the contralateral and ipsilateral brain regions relative to the cue location (**Supplemental**
207 **Figure 1**). ANOVAs indicated that there was higher contralateral than ipsilateral activity across
208 brain areas (endogenous: $F(1,4)=59.9$, $p=0.0015$; exogenous: $F(1,4)=218.8$, $p=0.0001$). For
209 both types of attention, this difference was more pronounced for valid than invalid cues (endog-
210 enous: $F(1,4)=8.6$, $p=0.04$; exogenous: $F(1,4)=21.1$, $p=0.01$). In the following analyses, we then
211 concentrate on fMRI activity in the contralateral ROIs to the attended location. **Supplemental**
212 **Figure 2** shows mean fMRI responses for a representative participant for each attention condi-
213 tion for two contralateral ROIs (V2 and LO1) relative to the cue. Response amplitude was ob-
214 tained from the target areas indicated in **Figure 2 (right panel)**.

215 We calculated an attentional modulation index: AMI = Vc / average (Vc + Ic + Vi + Ii),
216 which takes into account the overall response magnitude of each ROI. The AMI corresponds to
217 the ratio of the activity in contralateral ROIs for valid trials (Vc) over the average activity of con-
218 tralateral valid (Vc) and invalid trials (Ic), and distractor stimuli for pre and post-cue trials for
219 ipsilateral valid (Vi) and invalid trials (Ii). This AMI takes advantage of our fully factorial design.
220 We are isolating the activity brought about by the relevant attentional condition (valid trials in
221 endogenous or exogenous condition) and comparing it with the overall response magnitude
222 elicited by the presence of the stimuli regardless of attentional states. (Because some condition
223 values were negative, we added a fixed constant (0.2) to all condition values of each participant
224 before computing the AMI so that all resulting values were positive; see original values in **Fig-**
225 **ure 5.** Below we show that the pattern of results is the same for different constant values, indi-
226 cating that our results do not depend on the specific constant value we selected). A ratio of 1
227 would indicate no attentional modulation. The larger the AMI ratio, the higher the modulation in
228 the valid trials. We note that the AMI that we report cannot be directly compared with the AMI or
229 the values used by others, neither can the magnitude of the attentional modulation of previous
230 studies can be directly compared. From the list of the studies we include in Table 1, most use
231 group-average analyses, and statistics on contrasts between different conditions [51-53,64,78,79], and

232 two used ROI-based analyses but did not use AMI [42,65]. Other studies using ROI-based anal-
233 yses plot the different conditions individually, or differences between conditions (e.g. [32,70]), and
234 yet others use AMI indices but they differ among studies (e.g. [26,31,77,99]).

235 First, we showed that the AMI was significantly higher than 1 when combined across all
236 conditions and ROIs ($t(4) = 6.7$, $p = 0.0026$, Cohen's $d = 2.99$), and this was the case for each
237 participant. These results are consistent with previous findings showing that attentional orient-
238 ing increases fMRI signal in early visual cortex (for review [33]).

239 We then tested our two novel predictions: (1) attentional modulation of fMRI stimulus-
240 evoked activity increases along the visual hierarchy for endogenous pre-cueing, but is constant
241 for exogenous pre-cueing; and (2) attentional modulation of fMRI stimulus-evoked activity for
242 endogenous post-cueing is constant along the visual hierarchy, whereas there is no attentional
243 modulation for exogenous post-cueing. We first calculated the differences in activity between
244 valid and invalid trials for each type of attention and for pre- and post-cues, across the hierar-
245 chy of visual cortical areas. fMRI (AMI) responses were significantly larger for valid than invalid
246 cues, for both endogenous and exogenous cues, and for both pre- and post-cues. A three-way
247 repeated measures ANOVA (2 exogenous/endogenous x 2 pre/post-cue x 6 ROIs) of the differ-
248 ence between valid and invalid conditions revealed significant main effects of exoge-
249 nous/endogenous condition ($F(1,4) = 33.8$, $p = 0.0043$) and of ROI ($F(5,4) = 3.3$, $p = 0.0258$),
250 as well as an interaction between pre/post-cue and ROI ($F(5,4) = 3.5$, $p = 0.0192$). Thus, we
251 investigated modulations of fMRI activity separately for pre and post-cueing attention condi-
252 tions.

253 Linear mixed models [100] were then used to test: (1) an increase of fMRI activity along the
254 visual hierarchy for pre-cueing endogenous attention but not for exogenous attention, and (2)
255 post-cue attentional modulation of fMRI activity for post-cueing endogenous attention but not for
256 exogenous attention. We implemented two models, one for the pre-cueing and the other for the
257 post-cueing condition, to test the link between fMRI activity and the interaction between ROI
258 and endogenous/exogenous attention conditions. In each model, we entered as fixed effect the
259 ROI and the endogenous/exogenous conditions into the model, as well as their interaction. As

260 random effects, we had participant's intercepts and slopes for the effect of ROI and endoge-
261 nous/exogenous conditions. Visual inspection of residual plots did not reveal any obvious de-
262 viations from homoscedasticity or normality. P-values were obtained by likelihood ratio tests.
263 For the pre-cueing condition, we observed a significant effect of ROI (t(56)=3.5, p=0.0009, es-
264 timate=0.05±0.01, standard error), as well as a significant interaction between ROI and endog-
265 enous/exogenous conditions (t(56)=-2.3, p=0.025, estimate=-0.018±0.008, standard error). For
266 the post-cueing condition, we observed a significant effect of the fixed effect intercept
267 (t(56)=23.3, p<0.0001, estimate=11±0.05, standard error). Finally, we performed independent
268 regression analyses on each pre-/post-cueing and endogenous/exogenous attention conditions
269 (**Figure 3**). We observed a significant increase along the hierarchy of the visual areas of the
270 activity difference evoked by valid and invalid trials for the endogenous pre-cueing condition
271 (F(4)=16.5, p=0.015, R^2=0.81), but not for the exogenous pre-cueing condition (F(4)=1.8,
272 p=0.249, R^2=0.31), endogenous post-cueing (F(4)=2.2, p=0.216, R^2=0.35) or exogenous post-
273 cueing conditions (F(4)=0.3, p=0.61, R^2=0.07). See **Supplemental Figure 3** and **Supple-**
274 **mental Table 1 and 2,** which show the same pattern of results for different constant values,
275 indicating that our results do not depend on the specific value of the constant we selected.

276 Together, the results of the linear mixed models and the regression analyses (**Figure 3**)
277 showed differential effects between pre-/post-cueing and endogenous/exogenous attention
278 conditions. The AMI increases along the hierarchy of the visual areas in pre-cueing of endoge-
279 nous attention but not for pre-cueing of exogenous attention. Moreover, the AMI with post-
280 cueing of endogenous attention is constant along the hierarchy (significant intercept), but ab-
281 sent for post-cueing of exogenous attention. These analyses are consistent with post-hoc t-
282 tests performed for each condition and ROI in the AMI modulation (**Figure 4**). See **Supple-**
283 **mental Figure 4,** which shows the same pattern of results for the difference in fMRI activity (in
284 percent signal change) between valid and invalid.

285 For both endogenous attention (p < 0.05 for V2, V3, V3a, V4 and LO1; one-tailed t-tests)
286 and exogenous attention (p < 0.05 for V2, V3, V3A, hV4 and LO1; one-tailed t-tests) pre-cues
287 elicited greater fMRI activity for valid than invalid cues (**Figure 4**, top-left and top-right panels).

288 Furthermore, for endogenous attention ($p < 0.05$ for V1, V2, V3, V3A, hV4 and LO1; one-tailed
289 t-tests; **Figure 4**, bottom-left panel), but not for exogenous attention (all $p > 0.05$; one-tailed t-
290 tests; **Figure 4**, bottom-right panel), post-cues elicited greater fMRI activity for valid than invalid
291 cues in occipital areas (detailed statistics are presented in **Supplementary Table 3**). Critically,
292 these effects were consistently observed across participants (**Figure 5**). Taken together, these
293 results confirm both of our predictions.

294

295 **DISCUSSION**

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

302 Previous studies comparing endogenous and exogenous attention conditions state vari-
303 ous attentional effects in early visual areas (see **Table 1**). Some report differential effects be-
304 tween these attention conditions in the right LO and MT [52], others in the cuneus [51-53], the occipi-
305 tal gyrus (SOG, MOG, LOG; [52,53,64]), the fusiform area [52,64,65], and the TOS, LG and SC [64]. This
306 lack of clear picture regarding the differential impact of endogenous and exogenous spatial
307 attention is likely due to the methodological differences and limitations we discussed in the In-
308 troduction (see also **Table 1**). In any case, it is often assumed that the effects of endogenous
309 and exogenous attention are the same in visual occipital areas [33,38,39,50,51].

310 Other regions in striate and extra-striate visual areas could be implicated in both endoge-
311 nous and exogenous attention. For instance, area V6 has been reported to be involved in the
312 shift of covert attention, in both monkeys [101,102] and humans [103]. Because this area has a large
313 representation of the periphery [104], we would have needed a wider field of view than the one
314 we had to reliably define it. Similarly, higher-level visual areas are also involved in shifts of cov-

315 ert spatial attention, such as IPS 0 to IPS 5 (e.g. [31,39]). However, given the goal of our study,
316 and thus our slice prescription, we could not identify all IPS regions.

317 To further our knowledge of the neural correlates of attention, we investigated both atten-
318 tional orienting (valid cueing) and reorienting (invalid cueing), critical in an ever-changing envi-
319 ronment [42,80,81,94]. Furthermore, given ubiquitous performance tradeoffs between attended (ben-
320 efits) and unattended (costs) locations (e.g. [3,28,88-93]), we assessed activity at both attended
321 (contralateral ROI) and unattended (ipsilateral ROI) locations. Finally, we investigated how at-
322 tentional effects varied as a function of pre- and post-cueing, thus contrasting the neural corre-
323 lates of perceptual and post-perceptual processing of information.

324 The behavioral effects obtained in the scanner are consistent with psychophysical stud-
325 ies. The enhanced performance brought about by the valid, but uninformative peripheral pre-
326 cue is consistent with an automatic, bottom-up involuntary capture of exogenous attention (e.g.
327 [3,4,7,8,10,13,15,28,47,48,54,77,88,89,92,105,106]). The enhanced performance brought about by the valid, in-
328 formative central precue is consistent with a top-down, voluntary deployment of endogenous
329 attention (e.g. [3-8,11-13,26,28,47,48,54,87,92,107,108]).

330 In the endogenous attention condition, there was an increase in attentional modulation of
331 stimulus-evoked activity along the hierarchy of visual areas. There is no consensus regarding
332 the visual hierarchy beyond area V3 (e.g. [109-113]), especially regarding V3A. However, most au-
333 thors agree that hV4 precedes LO1 [109-112]. In any case, our data are consistent with either a
334 strict hierarchy or with V3A and hV4 being at the same level. Such a pattern is consistent with
335 previous studies suggesting that endogenous attention is a top-down modulation from frontal
336 and parietal areas feeding back to visual cortex, with diminishing effects in earlier visual areas
337 [31,39,82,83]. Inconsistent with previous studies (e.g. [26,28,32,114,115]), there was no evidence for atten-
338 tional modulation in V1. It might be that attentional modulation of V1 activity is more variable
339 than other visual cortical areas, making it harder to detect (see also [31,77]). Methodological differ-
340 ences between this and previous studies may have contributed to weakening the effect of at-
341 tention in V1. The accrual time in the current endogenous condition was relatively short (1300
342 ms in the valid condition and 500 ms in the invalid condition) compared to previous studies in-

343 vestigating endogenous, voluntary attention, in which the cue and/or stimuli were presented for
344 a long duration to maximize BOLD measurements (e.g. [26,28,32,114,115]). We chose the minimum
345 SOA (317 ms) at which performance benefits plateau to have as comparable conditions as
346 possible to the accrual time with the SOA for exogenous attention (117 ms). This short accrual
347 time may have limited the effects of attentional feedback to V1.

348 The fact that we do not see attentional modulation in V1 with our protocol may indicate
349 that V1 is not always necessary for attention to exert its behavioral effects. However, this null
350 result should not be over-interpreted so as to accept the null hypothesis. For example, the in-
351 consistent findings in the EEG literature regarding whether spatial attention can modulate V1
352 activity during the initial wave of visual processing depends on several factors (e.g., location,
353 presence of distractors, attentional load [116]). Similarly, some fMRI papers have shown signifi-
354 cant modulation of spatial attention in V1 (e.g. [26,28,32,114,115]). Furthermore, a recent study has
355 shown that TMS on the occipital pole (V1/V2) after attentional deployment eliminated the typical
356 benefits and costs brought about by exogenous attention at the respective attended and unat-
357 tended locations [89].

358 In the exogenous attention condition, in contrast to the endogenous attention, the atten-
359 tional modulation was approximately constant across the visual hierarchy. Some previous stud-
360 ies have reported a similar effect [117,118], others a decrease [119], and yet others an increase [77,120]
361 across the visual areas. This difference might be explained by different task parameters. For
362 example, in the Liu et al. (2005) study [77], participants knew which of the two stimuli was the
363 target they had to discriminate while the stimuli were presented, as one stimulus was vertical
364 and the other was tilted to the left or the right. In the present study, both stimuli were inde-
365 pendently tilted and participants had to wait for the response cue to appear to know which one
366 was the target and which one was the distractor.

367 Unlike in the endogenous pre-cueing condition in which the attention effect increased
368 along the processing stream, for the endogenous post-cueing effect there was no evidence that
369 the attentional modulation varied across these visual areas. The constant effect in the post-cue
370 condition could be due to the contribution of two counteracting factors: (1) the fMRI response

evoked by the stimulus in early visual areas may decrease along the visual hierarchy [121]; (2) the top-down modulations from frontal and parietal areas feedback to visual cortex with diminishing effects in earlier visual areas [26,31,39,82,83,122].

In the exogenous condition, there was no significant post-cueing effect on early visual areas. This result is consistent with that of Liu et al. (2005) [77], who while evaluating exogenous attention effects on occipital cortex included a post-cue condition to rule out sensory contamination of the cue (i.e. sensory response evoked by the cue itself) contributing to the enhanced BOLD activity found in their pre-cue condition. In addition to ruling out a possible sensory contamination, the present results show that, in contrast to endogenous attention, exogenous attention does not aid in the selective readout of information. Although there was no reliable modulation of exogenous post-cue on early and intermediate visual areas, in this study, it had an effect on behavior. Such effect is sometimes [71,72] but not always [73-76] observed. It is thus possible that our imaging protocol was not sensitive enough or that this behavioral effect is supported by higher order regions.

The ROI-based analysis that we followed here enabled us to compare contralateral and ipsilateral modulation of BOLD activity, thus providing additional information regarding the differences in processing dynamics of both types of attention. We observed a larger difference between contralateral and ipsilateral areas for the valid than the invalid cueing condition. This effect could be due to the fact that for the former, participants were attending to the same location throughout the trial, whereas for the latter, when the response cue did not match the pre-cue, participants had to switch their spatial attention to the opposite stimulus location, thus activity at that new location would be accumulated for less time. For instance, for endogenous attention, for the valid condition participants could have been processing the target for almost 500 ms before the response cue appeared. When the response cue matched the pre-cue, participants continued processing and reading out the signal from that location for up to 800 ms (they were not allowed 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 is invalid. Likewise, the larger modulatory effect for endogenous than exogenous attention is consistent with the difference in accrual time.

In a recent study [42] 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 such reorienting 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. 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.

426 **MATERIALS and METHODS**

427 The behavioral methods employed in this study and the behavioral results are the same
428 as those we reported in a recent study, in which we compared activity in TPJ during orienting
429 and reorienting of endogenous and exogenous attention [42]. To maximize the effects of these
430 two types of attention, i.e. the benefits at the attended location and concurrent costs at the un-
431 attended location, we used optimal spatial and temporal parameters (reviews by [1,2]). To enable
432 direct comparison between endogenous and exogenous attention, the same participants per-
433 formed the same orientation discrimination task under both types of attention. The fMRI meth-
434 ods employed in this study are the same as those used in that study [42], but here, instead of
435 analyzing TPJ activity, we analyzed activity in occipital areas.

436 **Participants**

437 Five participants (two male and three female, 24-30 years-old) participated in the study.
438 They all had normal or corrected-to-normal vision. The University Committee on Activi-
439 ties Involving Human Subjects at New York University approved the experimental protocol (IRB
440 # 10-7094), and participants provided written informed consent. All methods were performed in
441 accordance with US regulations and the Declaration of Helsinki. Our study used single-
442 participant ROI-based analysis, and thus had a small sample size. The same sample size that
443 has been used in many fMRI studies in our labs (e.g. [26,28,42,77,123-127]), as well as in other labs
444 (e.g. [128-132]). Each participant performed nine scanning sessions: one session to obtain a set of
445 three high-resolution anatomical volumes, two sessions for retinotopic mapping, three sessions
446 for the exogenous attention condition and three sessions for the endogenous attention condi-
447 tion (with the order counterbalanced among participants). Participants performed several prac-
448 tice sessions outside the scanner prior to the first scanning session of each attention condition.

449 **Stimuli**

450 Stimuli were generated on a Macintosh computer using the MGL toolbox [133] in MATLAB
451 (MathWorks). Stimuli were presented on a flat-panel display (NEC, LC-XG250 MultiSync LCD
452 2110; refresh rate: 60 Hz; resolution: 1024 x 768 pixels) positioned at the rear of the scanner

453 bore and housed in a Faraday box with an electrically conductive glass front. The display, cali-
454 brated and gamma corrected using a linearized lookup table, was at a viewing distance of 172
455 cm from the participant, and visible through an angled mirror attached to the head coil. A cen-
456 tral, white fixation cross (0.3°) was presented throughout the experiment. The two stimuli were
457 two 4-cpd gratings windowed by raised cosines (3° of diameter; 7% contrast), one in each bot-
458 tom quadrant (5° horizontal eccentricity; –2.65° altitude; 5.66° of eccentricity from the central
459 fixation to the stimulus center). Both endogenous cues and exogenous cues were white rectan-
460 gles (0.7°). The endogenous cues appeared adjacent to the fixation cross indicating one of the
461 two lower quadrants (0.35° horizontal eccentricity from the edge of the fixation cross, and 0.35°
462 altitude). The exogenous cues appeared adjacent to an upcoming grating stimulus, vertically
463 aligned with the stimulus and above the horizontal meridian (1° away from the edge of the grat-
464 ing stimulus; and the edge of the cue 4.44° horizontal eccentricity from the edge of the fixation
465 cross).

466 **Behavioral procedure**

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

479 In both exogenous and endogenous condition, cues were presented for 67 ms, indicat-
480 ing either the bottom left or right quadrant of the screen. The inter-stimulus interval (ISI) be-

tween the cue and the grating stimuli was 50 ms for exogenous and 250 ms for endogenous conditions, resulting in SOA of 117 ms and 317 ms. We used the same timings for pre- and post-cue conditions (e.g. [10,26,66,77]). 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 [47,134-136].

The behavioral effects of endogenous attention are sustained (e.g. [107]) and thus, as shown in ERP studies (e.g. [137]), 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. [10,26,66,77]). 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; [138]). 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 for endogenous attention (e.g. [3,139,140]); (2) the short tim-

508 ing and non-informative cue in the exogenous condition ensured that no voluntary component
509 could be involved in the exogenous attentional effect.

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

519 Eye position was monitored during all scanning sessions using an infrared video camera
520 system (Eyelink 1K, SR Research, Ottawa, Ontario, http://www.sr-research.com/EL_
521 1000.html). Trials in which the participants blinked or broke fixation (1.5° radius from central
522 fixation) at any point from fixation onset to response cue offset were identified and regressed
523 separately in the MRI analysis, and removed from the behavioral analysis (13% ± 4% of the
524 trials on average across all participants).

525 **MRI Procedure**

526 *Scanning*

527 Imaging was conducted on a 3T Siemens Allegra head-only scanner (Erlangen, Germa-
528 ny), using a Siemens NM-011 head coil (to transmit and receive) to acquire anatomical images,
529 a receive-only 8-channel surface coil array (Nova Medical, Wilmington, MA) to acquire func-
530 tional images. To minimize participants' head movements, padding was used.

531 For each participant, three high-resolution anatomic images were acquired in one scan-
532 ning session, using a T1-weighted magnetization-prepared rapid gradient echo (MPRAGE)
533 sequence (FOV = 256 x 256 mm; 176 sagittal slices; 1 x 1 x 1 mm voxels), and were co-
534 registered and averaged. Using FreeSurfer (public domain software;

535 http://surfer.nmr.mgh.harvard.edu), the gray matter was segmented from these averaged ana-
536 tomical volumes. All subsequent analyses were constrained only to voxels that intersected gray
537 matter.

538 T2*-weighted echo-planar imaging sequence (i.e. functional images; TR = 1750 ms; TE =
539 30 ms; flip angle = 90°) measured blood oxygen level-dependent (BOLD) changes in image
540 intensity [141]. In each volume, 28 slices covered the occipital and posterior parietal lobes and
541 were oriented 45° to the calcarine sulcus (FOV = 192 x 192 mm; resolution = 2 x 2 x 2.5 mm;
542 no gap). To align functional images from different sessions to the same high-resolution anatom-
543 ical volume for each participant, we acquired an additional T1-weighted anatomical images in
544 the same slices as the functional images (spin echo; TR = 600 ms; TE = 9.1 ms; flip angle =
545 90°; resolution = 1.5 × 1.5 × 3 mm) during each scanning session, and used them in a robust
546 image registration algorithm.

547 *MRI data pre-processing*

548 Imaging data were analyzed in MATLAB, using mrTools [142] and custom software. To al-
549 low longitudinal magnetization to reach steady state, the first eight volumes of each run were
550 discarded. Spatial distortion was corrected using the B0 static magnetic field measurements
551 performed in each session. The functional data were then motion corrected, the linear trend
552 was removed, and a temporal high-pass filter was applied (cutoff: 0.01 Hz) to remove slow
553 drifts and low-frequency noise in the fMRI signal.

554 *Retinotopic mapping*

555 We followed well-established conventional traveling-wave, phase-encoded methods. Us-
556 ing clockwise and counter-clockwise rotating checkerboard wedges, we measured phase maps
557 of polar angle. Using contracting and expending checkerboard rings, we measured eccentricity
558 maps [95-98]. **Figure 2** (left panel) shows the visual areas of interest that were drawn by hand on
559 flattened surface of the brain, following published conventions [97,98,124,143].

560

561 *Stimulus localizer*

In each scanning session of the main experiment, participants completed one stimulus localizer run (6 runs overall, 4 min each). A run consisted of 16 cycles (17.5 s) of a block alternation protocol between stimulus on (8.75 s) and stimulus off (8.75 s). Participants only had to fixate the 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 [144], 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 3, 4 and 5) are made available via OSF at [link provided upon acceptance of the manuscript].

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Figures

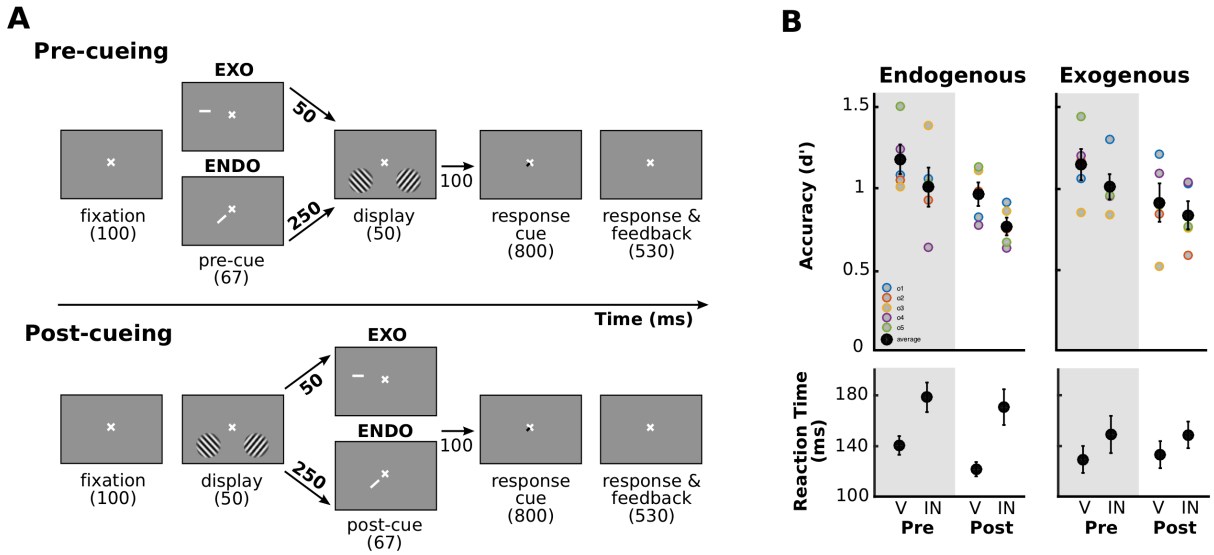


Figure 1. Experimental protocol. A. Participants performed a 2-AFC orientation-discrimination task. Pre-cues and post-cues were presented before and after the stimuli, respectively. Exogenous cues appeared in the periphery, above one of the two stimulus locations. Endogenous cues appeared at the center 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.

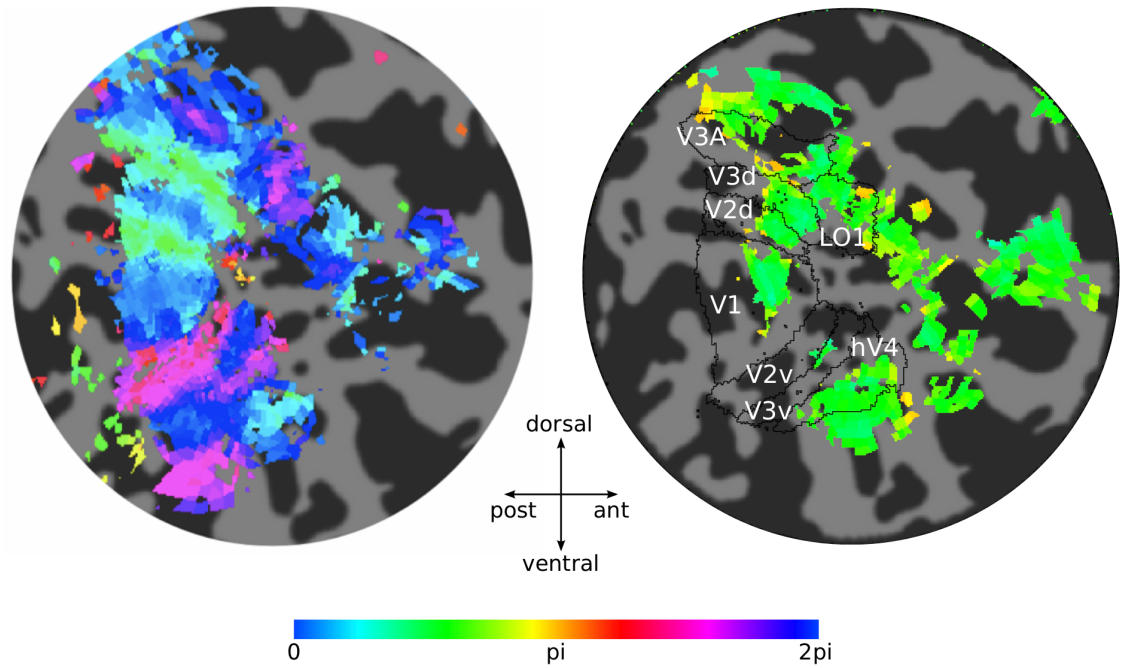


Figure 2. Retinotopic mapping and stimulus localizer of a representative participant. A flattened representation of the right hemisphere occipital pole. **Left,** map of polar angle. The color of each voxel in the map represents the response phase of the time series elicited by a rotating wedge stimulus. **Right,** stimulus localizer. The black outlines correspond to the retinotopic areas of interest (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.

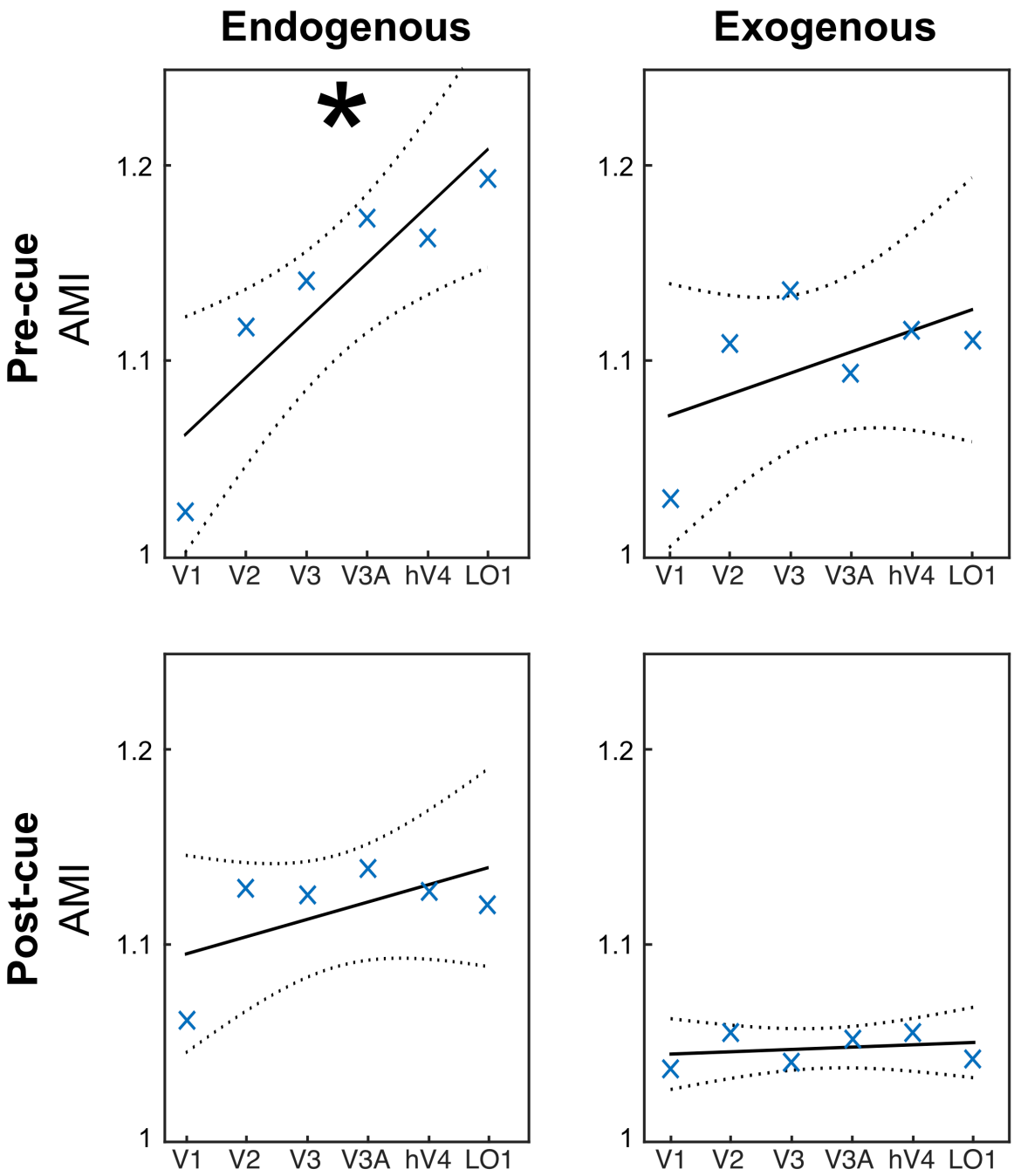


Figure 3. Specificity of pre and post-cueing for endogenous and exogenous attention. AMI, Attentional Modulation Index separately for pre- and post-cue conditions for each ROI: AMI = Vc / average (Vc + Ic + Vi + Ii). Vc, valid trials in contralateral ROI. Ic, invalid trials in contralateral ROI. Vi, valid pre- and post-cue trials in ipsilateral ROI. Ii, invalid pre- and post-cue trials in ipsilateral ROI. The larger this ratio, the higher the modulation in the valid trials. *, Statistically significant regression analysis ($p < 0.05$).

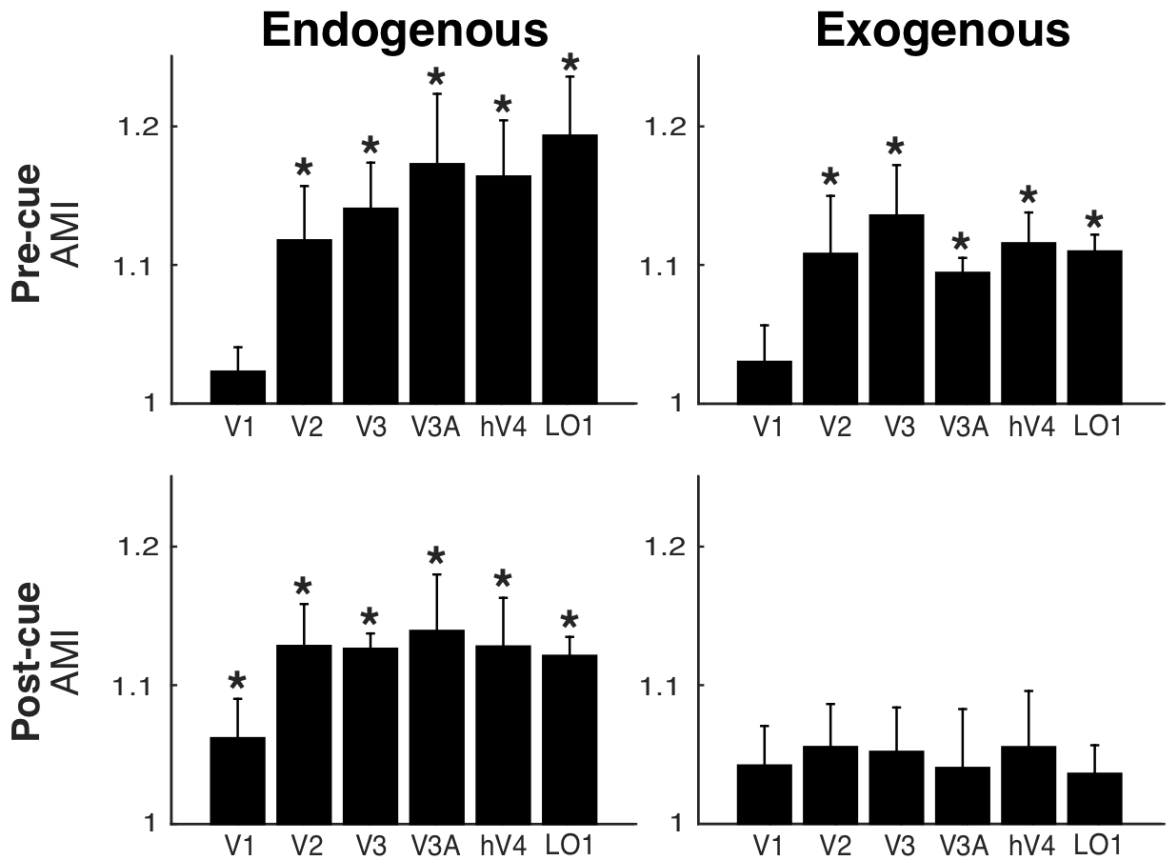
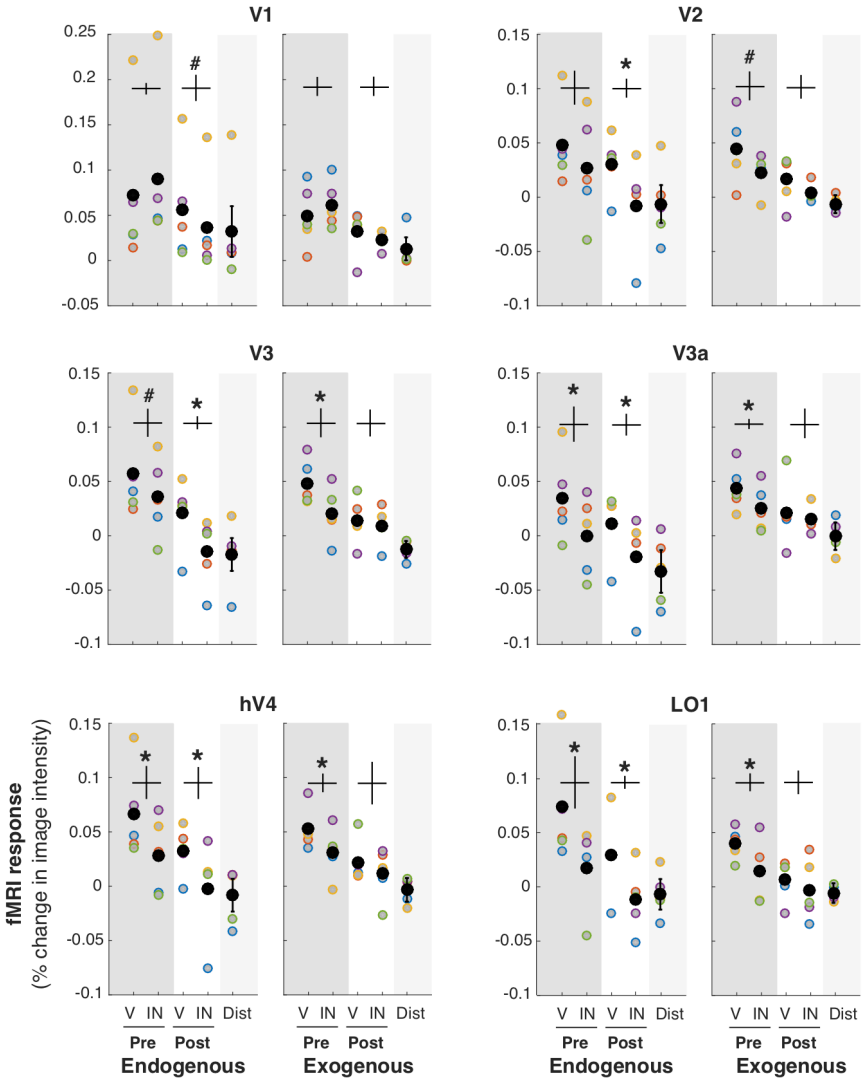


Figure 4. Single ROI responses for pre and post-cueing and for both endogenous and exogenous attention. The AMI is plotted separately for pre and post-cue conditions for each ROI (same data as in Figure 3). *, Statistically significant difference between valid and invalid, separately for pre and post-cueing ($p < 0.05$). Error bars on plots are ± 1 SEM.



977

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