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

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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 and bottom-up processing, visual perception.

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 Carrasco, 2011; Carrasco and Barbot, 2015). These two types of attention often have similar perceptual consequences (reviews by Carrasco, 2011; Carrasco and Barbot, 2015), 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. Sperling and Melchner, 1978; Kinchla, 1980; Giordano et al., 2009); (b) The effects of covert attention on contrast sensitivity often differ for endogenous and exogenous attention (e.g. Dosher and Lu, 2000; Ling and Carrasco, 2006a; Pestilli et al., 2009; Barbot et al., 2012); 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. Yeshurun and Carrasco, 1998; Carrasco et al., 2006; Yeshurun et al., 2008; Barbot and Carrasco, 2017; Jigo and Carrasco, 2018).

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 Carrasco and Yeshurun, 2009; Carrasco, 2011; Anton-Erxleben and Carrasco, 2013; Carrasco and Barbot, 2015). Specifically, single-unit studies in monkeys have demonstrated effects of endogenous attention in occipital areas (e.g. McAdams and Maunsell, 1999; Reynolds et al., 2000; Martínez-Trujillo and Treue, 2002; Williford and Maunsell, 2006; Mitchell et al., 2009; Reynolds and Heeger, 2009; Ruff and Cohen, 2014; Luo and Maunsell, 2015). Additionally, fMRI studies have shown that endogenous attention causes a baseline shift in early visual areas (e.g. Kastner et

al., 1999; Somers et al., 1999; O'Connor et al., 2002; Buracas and Boynton, 2007; Murray, 2008; Herrmann et al., 2010; Pestilli et al., 2011; review by Beck and Kastner, 2014) and increases the dynamic range of fMRI responses (Li et al., 2008; Lu et al., 2011). Comparatively, little is known about the effect of exogenous attention on visual areas both from single-unit studies (Busse et al., 2008; Wang et al., 2015) and fMRI studies (for reviews see Carrasco, 2011; Anton-Erxleben & Carrasco, 2013).

Since Corbetta and Schulman's seminal review (2002) 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 Chica et al., 2013; Beck and Kastner, 2014). Yet, there remains considerable debate regarding the dissociation between dorsal regions, for endogenous attention, and ventral regions, for exogenous attention (e.g. Hahn et al., 2006; Bowling et al., 2019), including the role of the temporo-parietal junction (TPJ; Doricchi et al., 2010; Geng and Vossel, 2013; Silvetti et al., 2015; Dugué et al., 2017a). Classically, researchers have described endogenous attention as a top-down process, and exogenous attention as a bottom-up process (e.g., Posner et al., 1980; Nakayama and Mackeben, 1989; Corbetta and Shulman, 2002; Hahn et al., 2006; Beck and Kastner, 2009; Carrasco, 2011; Chica et al., 2013; Beck and Kastner, 2014; Bowling et al., 2019). 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 Beck and Kastner, 2009; Carrasco, 2011; Chica et al., 2013; Beck and Kastner, 2014).

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 (Buschman and Miller, 2009; Bowling et al., 2019). 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 (Corbetta and Shulman, 2002; Peelen et al., 2004; Corbetta et al., 2008; Chica et al., 2013; Beck and Kastner, 2014).

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 (see **Table 1**):

(1) The effect of attention on behavioral performance was assessed in some studies with a detection task using RT as their only dependent variable (Mayer et al., 2004; Peelen et al., 2004; Natale et al., 2006), in which performance may differ due to speed of processing, discriminability or criterion (Reed, 1973; Wickelgren, 1977; Carrasco and McElree, 2001) and/or motor behavior (Correa et al., 2010; Yashar and Lamy, 2011).

(2) In the studies in which performance was assessed in a discrimination task using RT (Kim et al., 1999; Kincade et al., 2005; Esterman et al., 2008), small RT differences were reported, which could have resulted from speed of processing, discriminability, or criterion factors (Reed, 1973; Wickelgren, 1977; Carrasco and McElree, 2001).

(3) In the studies in which accuracy was not assessed (Rosen et al., 1999; Mayer et al., 2004; Peelen et al., 2004; Natale et al., 2006), 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 (Culham et al., 2001; Herath et al., 2001).

(4) For the studies in which eye position was not monitored while participants performed the task in the scanner (Kim et al., 1999; Rosen et al., 1999; Mayer et al., 2004; Peelen et al., 2004; Kincade et al., 2005; Natale et al., 2006; Meyer et al., 2018; Bowling et al., 2019), the results could be due to covert attention, overt attention or both (Carrasco et al., 1995; Beauchamp et al., 2001; Carrasco, 2011).

(5) Given that exogenous attention is a fast, transient process (for review see Carrasco, 2011; Carrasco and Barbot, 2015), it was inappropriately manipulated in the studies in which long stimulus onset asynchronies (SOA) were used (Rosen et al., 1999; Peelen et al., 2004; Kincade et al., 2005; Natale et al., 2006; Esterman et al., 2008) 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; Esterman et al., 2008) and the other in the TPJ (Dugué et al., 2017), 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 (Mayer et al., 2004; Peelen et al., 2004; Kincade et al., 2005; Natale et al., 2006), 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 areas, and how modulation of activity in visual cortex is linked to changes in perceptual performance. (See Dugué and colleagues (Dugué et al., 2017a), 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 (Kinchla et al., 1995; Nobre et al., 2004a; Ruff et al., 2007; Hulme et al., 2009) and modulate fMRI activity in early visual areas (Nobre et al., 2004a; Hulme et al., 2009; Pestilli et al., 2011; Sergent et al., 2011). Exogenous post-cues also affect performance in some tasks (Sergent et al., 2013; Thibault et al., 2016), but not in others (Carrasco and Yeshurun, 1998; Gobell and Carrasco, 2005; Anton-Erxleben et al., 2007; Fuller et al., 2009), and the only study evaluating post-cues in exogenous attention showed no such modulation (Liu et al., 2005). 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								
Mayer et al., 2004	central arrow 70% valid	luminance change of peripheral place-holder 50% valid SOA=100 or 800 ms	X	RT	Group-averaged	**Occipital:** *Cuneus, MOG, SOG* + Frontal Temporo-Parietal	No	No
Peelen et al., 2004	central arrow 75% valid	brightening of pe-ripheral placeholder 50% valid SOA=550 ms	square	RT	Group-averaged	**Occipital:** *Cuneus* + Frontal Temporo-Parietal	No	No
Natale et al., 2006	single peripheral rectangular frame 100% valid	five peripheral rec-tangular frames 20% valid SOA=8, 8.15, 8.3, 8.45 or 8.6 s	a black and white check-erboard	RT *for 4 out of 8 participants*	Group-averaged	**Occipital:** *Fusiform, TOS, LG, SC, LOG* + Frontal Temporo-Parietal	No	No
Discrimination tasks								
Kincade et al., 2005	brightening of half of central fixation diamond 75% valid	color singleton in an array of colored squares 50% valid SOA=2160 ms	T vs. L	RT (% correct)	Group-averaged	**Occipital:** *LO, MT, Cuneus, Fusiform, SOG* + Frontal Temporo-Parietal	No	No
Esterman et al., 2008	color change of a peripheral place-holder 75% valid	50% valid SOA=300 ms	face identity	RT (% correct)	ROI-based (FFA) + Group-averaged	**Occipital:** *FFA* + Frontal Temporo-Parietal	Yes	No
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								
Rosen et al., 1999	central arrow 80% valid	peripheral dot 50% valid SOA=400, 550 or 700 ms	filling of a square	RT	Group-averaged	Frontal Temporo-Parietal	No	No

Discrimination tasks								
Kim et al., 1999	thickening of part of central fixation diamond 80% valid SOA=200, 400 or 800 ms	luminance change of peripheral place-holder 50% valid SOA= 100, 150 or 200 ms	X vs. +	RT (% correct)	Group-averaged	Frontal Temporo-Parietal	No	No
Meyer et al., 2018	color change of central fixation 83% valid SOA=700–1000 ms	whitening of periph-eral placeholder 50% valid SOA=100–300 ms	central color of a check-erboard	Inverse efficiency = RT/%correct	Group-averaged	Frontal Temporo-Parietal	No	No
Dugué et al., 2017	central bar 75% invalid SOA=310 ms	peripheral bar 50% valid SOA=110 ms	orientation	d-prime (RT)	ROI-based	Temporo-Parietal	Yes	No
Bowling et al., 2019	color change of central fixation 83% valid SOA=700–1000 ms	whitening of periph-eral placeholder 50% valid SOA=100–300 ms	central color of a check-erboard	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.*

155 Here, with the same participants, task, stimuli and task difficulty for all attention manipu-
156 lations, we tested the following four predictions: (1) Pre-cueing should induce an attentional mod-
157 ulation of fMRI activity, higher in the valid than the invalid condition in which attention needs to
158 be reoriented to the opposite location to perform the task (e.g., Liu et al., 2005). (2) Both endog-
159 enous and exogenous pre- and post-cueing effects should be stronger in visual regions contra-
160 lateral to the attended hemifield (e.g., Liu et al., 2005; Serences and Yantis 2007; Pestilli et al.,
161 2011). (3) Pre-cueing endogenous attention, but not exogenous attention, should increase activ-
162 ity modulations along the visual hierarchy (e.g., higher in V4 than in V1; Kastner et al., 1999;
163 Pestilli et al., 2011; for reviews Chica et al., 2013; Beck and Kastner, 2014). For endogenous
164 attention, a top-down process, modulations from higher-order, fronto-parietal attentional regions
165 would send feedback information to visual cortex with diminishing effects in earlier visual areas,
166 given the increased distance from the source. (4) Post-cueing endogenous (Nobre et al., 2004b;
167 Hulme et al., 2009; Pestilli et al., 2011; Sergent et al., 2011), but not exogenous (Liu et al., 2005),
168 attention should induce attentional modulation of fMRI activity in early visual areas. Voluntary,
169 endogenous attention would facilitate reading out perceptual information (Dugué et al., 2017a),
170 and modulate its processing (Nobre et al., 2004a; Hulme et al., 2009; Pestilli et al., 2011; Sergent
171 et al., 2011). The only fMRI study assessing the effects of post-cueing exogenous attention found
172 no attentional modulation of fMRI activity in early visual areas (Liu et al., 2005); some behavioral
173 studies report post-cueing effects (Sergent et al., 2013; Thibault et al., 2016) but others found no
174 such effects (Carrasco and Yeshurun, 1998; Gobell and Carrasco, 2005; Anton-Erxleben et al.,
175 2007; Fuller et al., 2009).
176 To test these four predictions, we measured fMRI activity and compared the effects of
177 endogenous and exogenous attention in early visual areas while the same participants performed
178 the same task –a 2-AFC orientation discrimination task, contingent upon contrast sensitivity
179 (Nachmias, 1967; Carrasco et al., 2000; Pestilli et al., 2009). We used a fully-crossed design:
180 two attention conditions –endogenous or exogenous attentional orienting– and two types of cue-
181 ing –pre- or post-cue. We evaluated fMRI activity at both the attended and the un-attended loca-
182 tions, given the ubiquitous performance tradeoffs at attended (benefits) and unattended (costs)

183 locations compared to a neutral condition (e.g. Luck et al., 1994; Lu and Dosher, 1998; Pestilli
184 and Carrasco, 2005; Giordano et al., 2009; Montagna et al., 2009; Herrmann et al., 2010; Ye-
185 shurun and Rashal, 2010), and the importance of evaluating both the orienting and reorienting of
186 attention (Dugué et al., 2016; 2017a; Senoussi et al., 2019), critical in an ever-changing environ-
187 ment (Dugué et al., 2016; 2017b).

188 This is the first study to systematically evaluate and directly compare how pre and post-
189 orienting, and reorienting, of endogenous and exogenous attention modulate neural activity in
190 visual cortex to affect behavior. The results indicate that these two types of spatial covert attention
191 distinctly modulate activity in individual retinotopic visual cortical areas. These differences in ac-
192 tivity are consonant with differential engagement of top-down and bottom-up processes and their
193 respective temporal dynamics. These results suggest that endogenous attention facilitates both
194 the encoding and the readout of visual information whereas exogenous attention only facilitates
195 the encoding of information.

196

197 **RESULTS**

198 **Endogenous and exogenous attention improve performance**

199 Participants performed a 2-AFC orientation-discrimination task under two attentional con-
200 ditions (exogenous or endogenous attention), when the cue was presented either before (pre-
201 cue) or after (post-cue) the grating stimuli (see Methods), and while their brain activity was meas-
202 ured with fMRI (**Figure 1**). The cue was either valid or invalid (50/50% of the time in the exoge-
203 nous condition, and 75/25% in the endogenous condition, respectively).

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

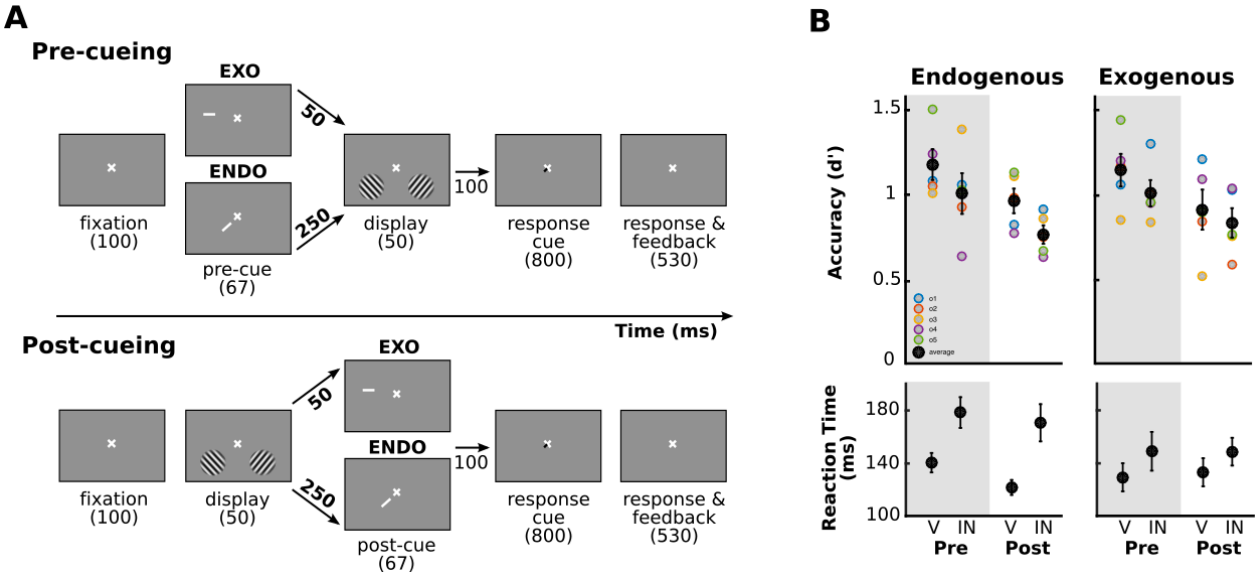

Figure 1. Experimental protocol. A. *Participants performed a 2-AFC orientation-discrimination task. (The display is not at scale for visibility purposes). Pre-cues and post-cues were presented before and after the stimuli, respectively. Exogenous cues appeared in the periphery, above one of the two stimulus locations. Endogenous cues appeared at the center of the screen 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 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 (Lu and Dosher, 1998; Carrasco et al., 2000; Dosher and Lu, 2000; Ling and Carrasco, 2006b; Giordano et al., 2009; Pestilli et al., 2009; Herrmann et al., 2010), 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., Engel et al., 1994; Sereno et al., 1995; Engel et al., 1997; Larsson and Heeger, 2006; Wandell et al., 2007).

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.

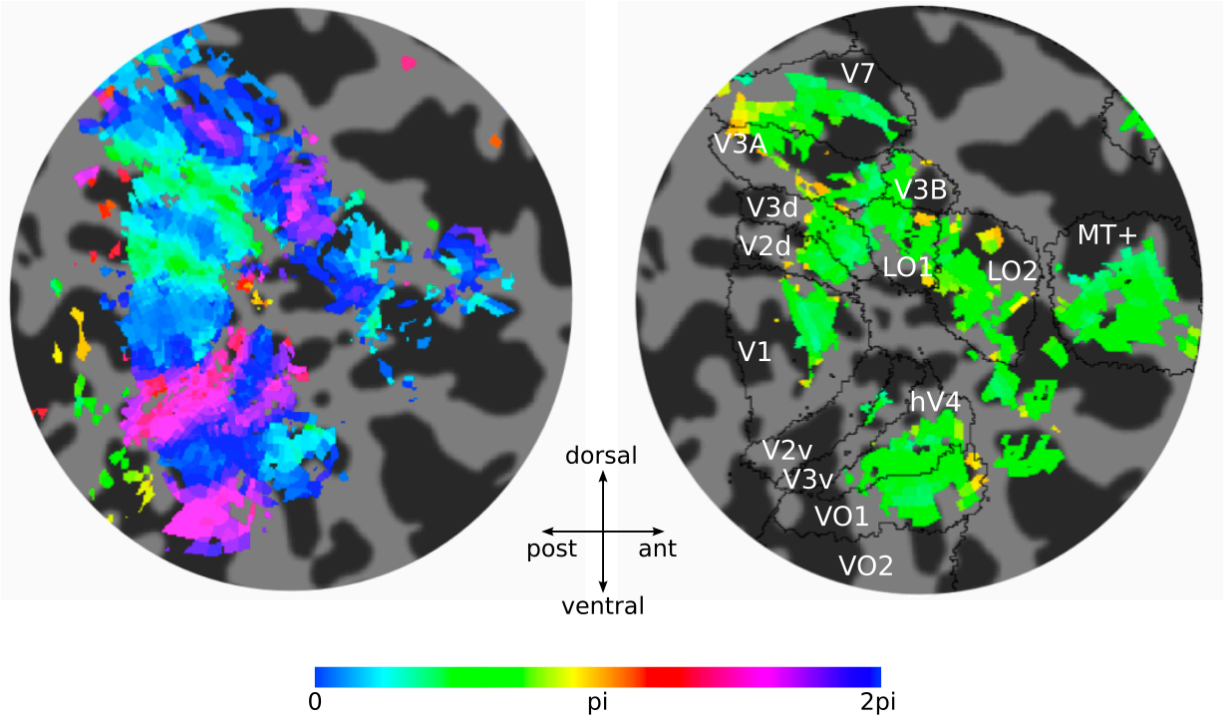

Figure 2. Retinotopic mapping and stimulus localizer of a representative participant. *A flattened representation of the right hemisphere occipital pole.* ***Left,*** *map of polar angle. The color of each voxel in the map represents the response phase of the time series elicited by a rotating wedge 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 (Ress et al., 2000; Giesbrecht et al., 2006; Liu et al., 2007a), and that attentional orienting increases fMRI signal in early visual cortex (for review Beck and Kastner, 2014).

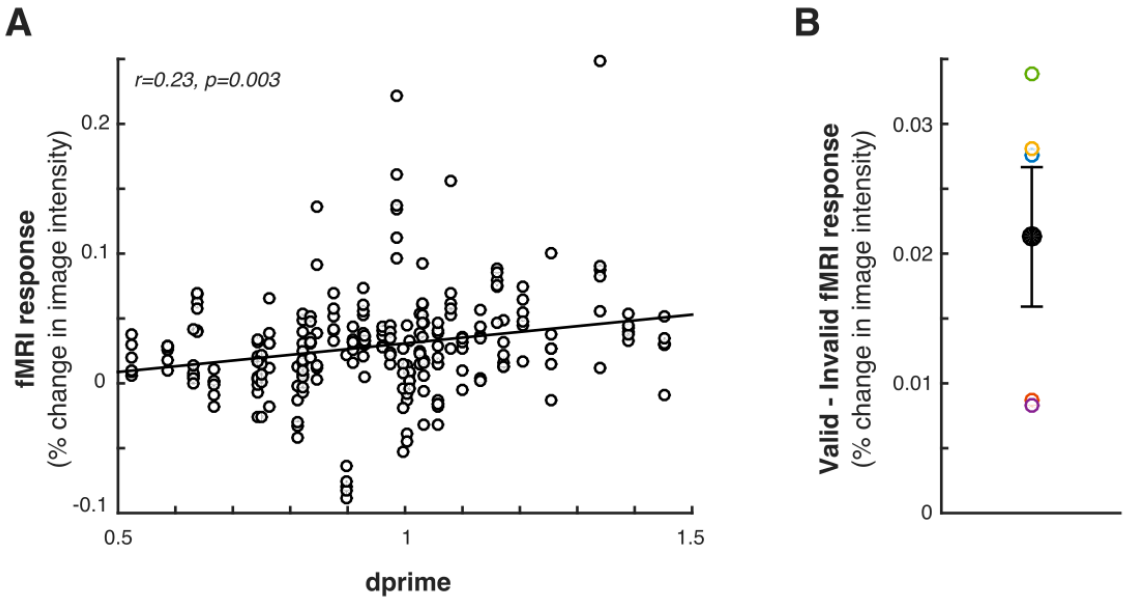

Figure 3. Inter-individual fMRI response. A. *Positive correlation between fMRI response and behavioral performance (Pearson correlation r = 0.23, p = 0.003). Each dot indicates fMRI response amplitude measured from one ROI and one participant, separately for each attentional condition (pre and post-cue, 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 (**Figure 4**). Regression analyses showed 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 ($F = 0.1$, $p = 0.774$, $R^2 = 0.02$). The differential effects of these regression analyses are consistent with post-hoc t-tests performed for each condition and ROI (**Figure 5**).

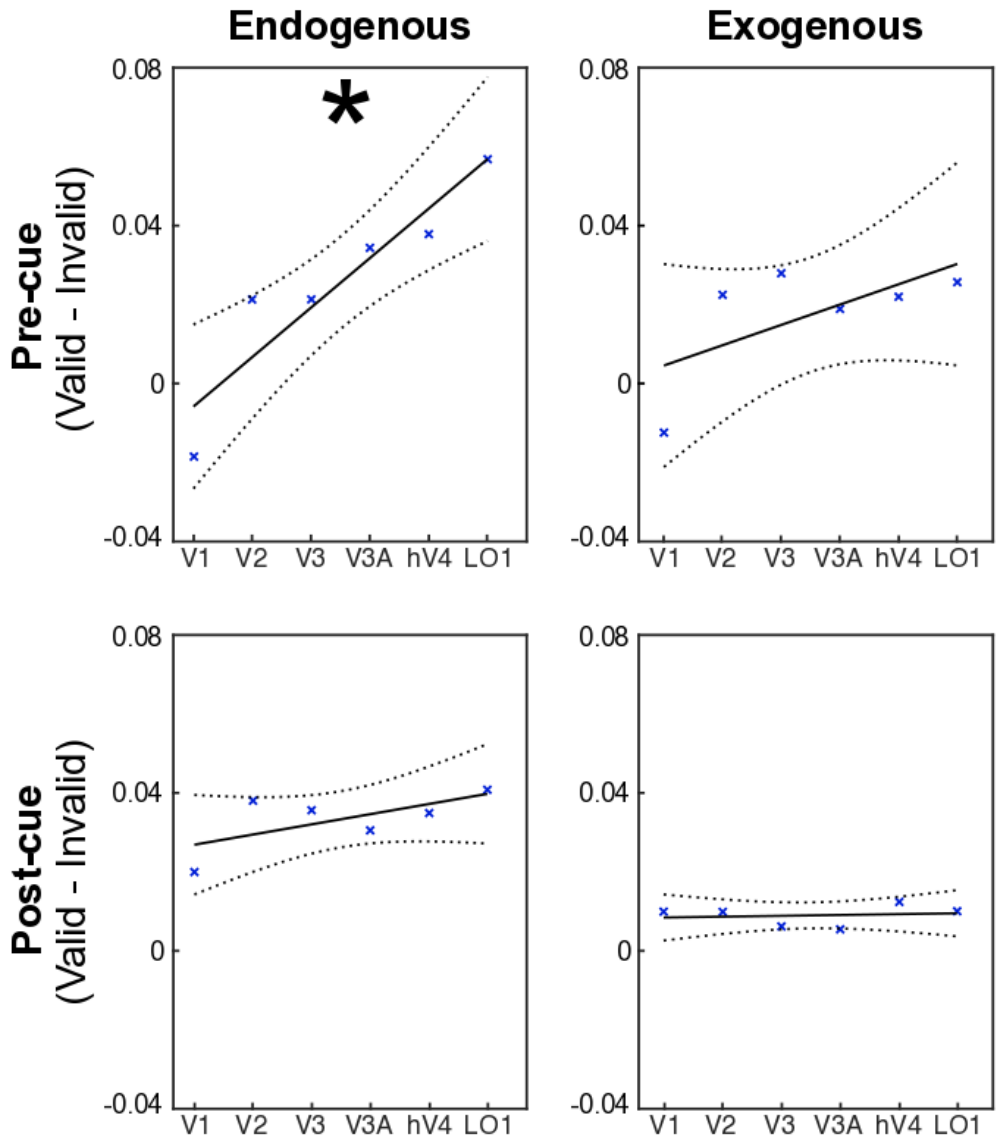

Figure 4. Specificity of pre and post-cueing for endogenous and exogenous attention. *The difference in fMRI response between valid and invalid is plotted separately for pre- and post-cue conditions for each ROI. *, Statistically significant regression analysis (p < 0.05).*

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). Taken together, these results confirm both of our predictions.

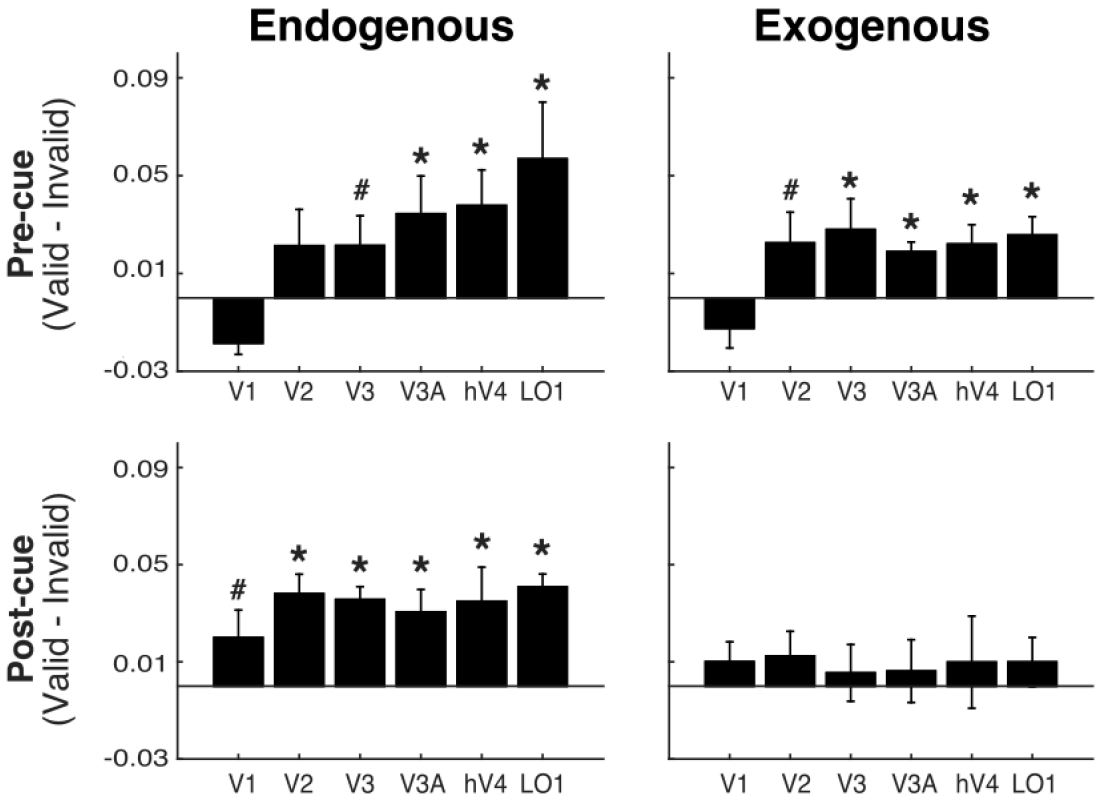

Figure 5. Single ROI responses for pre and post-cueing and for both endogenous and exogenous attention. *The difference in fMRI response between valid and invalid is plotted separately for pre and post-cue conditions for each ROI. *, Statistically significant difference between valid and invalid, separately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

These effects were consistently observed across participants (**Figure 6**). 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 ($F = 4.1$, $p = 0.0103$).

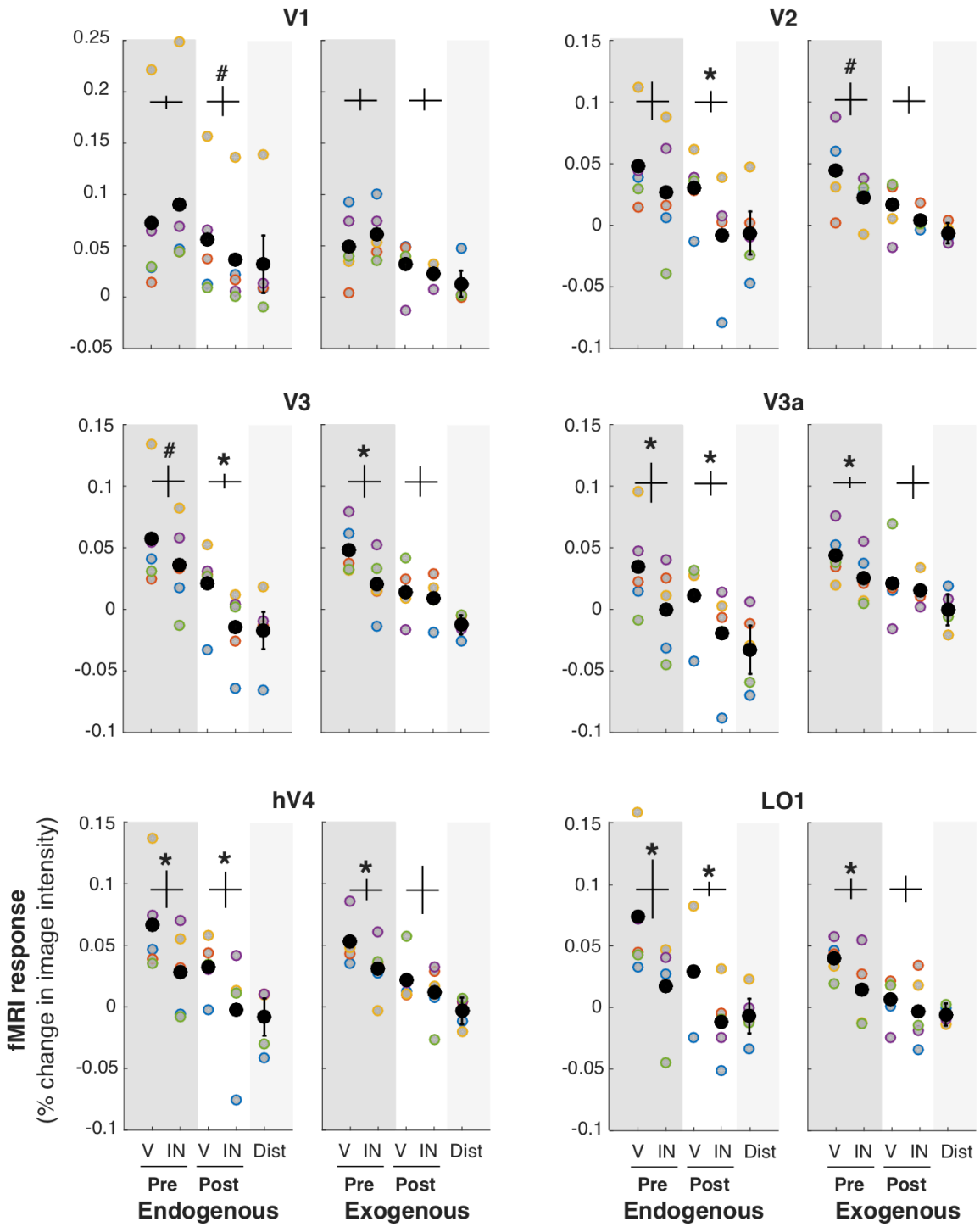

Figure 6. Specificity of each visual ROI for endogenous and exogenous attention. *fMRI response amplitude was measured for each attentional condition. V: valid cue condition (target location matches the location indicated by pre-cue/post-cue). IN: invalid cue condition (target location at the opposite 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 (Kincade et al., 2005), others in the cuneus (Peelen et al., 2004; Mayer et al., 2004; Kincade et al., 2005), the occipital gyrus (SOG, MOG, LOG; Mayer et al., 2004; Kincade et al., 2005; Natale et al., 2006), the fusiform area (Kincade et al., 2005; Natale et al., 2006; Esterman et al., 2008), and the TOS, LG and SC (Natale et al., 2006). 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 (Corbetta and Shulman, 2002; Peelen et al., 2004; Corbetta et al., 2008; Chica et al., 2013; Beck and Kastner, 2014).

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 (e.g. Dugué et al., 2016; 2017b; Senoussi et al., 2019). Furthermore, given ubiquitous performance tradeoffs between attended (benefits) and unattended (costs) locations (e.g. Pestilli and Carrasco, 2005; Giordano et al., 2009; Montagna et al., 2009; Herrmann et al., 2010; Fernández et al., 2019), 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 (Ress et al., 2000; Giesbrecht et al., 2006; Liu et al., 2007a). The behavioral effects obtained in the scanner are consistent with psychophysical studies. The enhanced performance brought about by the valid, but uninformative peripheral pre-cue is consistent with an automatic, bottom-up involuntary capture of exogenous attention (e.g. Dosher and Lu, 2000; Carrasco et al., 2000; Carrasco et al., 2004; Pestilli and Carrasco, 2005; Giordano et al., 2009; Herrmann et al., 2010; Fernández et al., 2019). The enhanced performance brought about by the valid, informative central precue is consistent with a top-down, voluntary deployment of endogenous attention (e.g. Dosher and Lu, 2000; Ling and Carrasco, 2006c; Giordano et al., 2009; Liu et al., 2009; Herrmann et al., 2010; Poletti et al., 2017; Jigo and Carrasco, 2018).

In the endogenous attention condition, there was an increase in attentional modulation of stimulus-evoked activity along the hierarchy of visual areas. There is no consensus regarding the visual hierarchy beyond area V3 (e.g. Harvey and Dumoulin, 2011; Harvey and Dumoulin, 2016; Michalareas et al., 2016; Yildirim et al., 2018; Fritsche et al., 2020), especially regarding V3A. However, most authors agree that hV4 precedes LO1 (Harvey and Dumoulin, 2011; Harvey and Dumoulin, 2016; Michalareas et al., 2016; Yildirim et al., 2018). In any case, our data are consistent with either a strict hierarchy or with V3A and hV4 being at the same level. Such a pattern is consistent with previous studies suggesting that endogenous attention is a top-down modulation from frontal and parietal areas feeding back to visual cortex, with diminishing effects in earlier visual areas (Kastner et al., 1999; Maunsell and Cook, 2002; Kastner and Pinsk, 2004; Chica et al., 2013). Inconsistent with previous studies (e.g. Boynton et al., 1999; Brefczynski and DeYoe, 1999; Somers et al., 1999; Herrmann et al., 2010; Pestilli et al., 2011), there was no evidence for attentional modulation in V1. It might be that attentional modulation of V1 activity is more variable than other visual cortical areas, making it harder to detect (see also Kastner et al., 1999; Liu et al., 2005). Methodological differences between this and previous studies may have contributed

397 to weakening the effect of attention in V1. The accrual time in the current endogenous condition
398 was relatively short (1300 ms in the valid condition and 500 ms in the invalid condition) compared
399 to previous studies investigating endogenous, voluntary attention, in which the cue and/or stimuli
400 were presented for a long duration to maximize BOLD measurements (e.g. Boynton et al., 1999;
401 Brefczynski and DeYoe, 1999; Somers et al., 1999; Pestilli et al., 2011). We chose the minimum
402 SOA (317 ms) at which performance benefits plateau to have as comparable conditions as pos-
403 sible to the accrual time with the SOA for exogenous attention (117 ms). This short accrual time
404 may have limited the effects of attentional feedback to V1.

405 In the exogenous attention condition, in contrast to the endogenous attention, the atten-
406 tional modulation was approximately constant across the visual hierarchy. Some previous studies
407 have reported a similar effect (Müller and Kleinschmidt, 2007; Müller and Ebeling, 2008), others
408 a decrease (Heinen et al., 2011), and yet others an increase (Liu et al., 2005; Mulckhuyse et al.,
409 2011) across the visual areas. This difference might be explained by different task parameters.
410 For example, in the Liu et al. (2005) study, participants knew which of the two stimuli was the
411 target they had to discriminate as soon as the stimuli were displayed; one stimulus was vertical
412 and the other was tilted to the left or the right. In the present study, both stimuli were inde-
413 pendently tilted and participants did not know which one was the target and which one was the
414 distractor until later when the response cue appeared.

415 Unlike in the endogenous pre-cueing condition in which the attention effect increased
416 along the processing stream, for the endogenous post-cueing effect there was no evidence that
417 it varied across these visual areas. The constant effect in the post-cue condition could be due to
418 the contribution of two counteracting factors: (1) the fMRI response evoked by the stimulus in
419 early visual areas may decrease along the visual hierarchy (Kay et al., 2013b); (2) the top-down
420 modulations from frontal and parietal areas feedback to visual cortex with diminishing effects in
421 earlier visual areas (Chica and Lupiáñez, 2009; Kastner et al., 1999; Pestilli et al., 2011).

422 In the exogenous condition, there was no significant post-cueing effect on early visual
423 areas. This result is consistent with that of Liu et al. (2005), who while evaluating exogenous
424 attention effects on occipital cortex included a post-cue condition to rule out sensory

425 contamination of the cue (i.e. sensory response evoked by the cue itself) contributing to the en-
426 hanced BOLD activity found in their pre-cue condition. In addition to ruling out a possible sensory
427 contamination, the present results show that, in contrast to endogenous attention, exogenous
428 attention does not aid in the selective readout of information.

429 The ROI-based analysis that we followed here enabled us to compare contralateral and
430 ipsilateral modulation of BOLD activity, thus providing additional information regarding the differ-
431 ences in processing dynamics of both types of attention. We observed a larger difference be-
432 tween contralateral and ipsilateral areas for the valid than the invalid cueing condition. This effect
433 could be due to the fact that for the former, participants were attending to the same location
434 throughout the trial, whereas for the latter, when the response cue did not match the pre-cue,
435 participants had to switch their spatial attention to the opposite stimulus location, thus activity at
436 that new location would be accumulated for less time. For instance, for endogenous attention, for
437 the valid condition participants had been processing the target for almost 500 ms before the
438 response cue appeared. When the response cue matched the pre-cue, participants continued
439 processing and reading out the signal from that location for up to 800 ms (they were not allowed
440 to give an answer before the end of the response cue period). But when the response cue did
441 not match the pre-cue, then participants had to switch after 500 ms to the other location (ipsilat-
442 eral) thus accumulating less activity. Similarly, the accumulation time for the invalid cue condition
443 in exogenous attention was only about 300 ms. This accrual time explanation could also account
444 for the larger difference between contralateral and ipsilateral for pre-cues than post-cues, i.e.
445 there is a 300 ms accumulation when the exogenous pre-cue is invalid, while only 100 ms when
446 the post-cue in invalid. Likewise, the larger modulatory effect for endogenous relative to exoge-
447 nous attention is consistent with the difference in accrual time.

448 The results of the present study complement our recent study (Dugué et al., 2017a) in
449 which we demonstrated that sub-regions of the Temporo-Parietal Junction (TPJ) that respond
450 specifically to visual stimuli are more active when attention needs to be spatially reoriented (in-
451 valid cueing) than when attention remains at the cued location (valid cueing), and that partially
452 overlapping specific visual sub-regions mediate reorienting after orienting of endogenous or

exogenous attention. Together, these two 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.

In 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.

MATERIALS and METHODS

The behavioral methods employed in this study and the behavioral results are the same as those we reported in a recent study, in which we compared activity in TPJ during orienting and reorienting of endogenous and exogenous attention (Dugué et al., 2017a). To maximize the effects of these two types of attention, i.e. the benefits at the attended location and concurrent costs at the unattended location, we used optimal spatial and temporal parameters (reviews by Carrasco, 2011; Carrasco and Barbot, 2015). To enable direct comparison between endogenous and exogenous attention, the same participants performed the same orientation discrimination task under both types of attention. The fMRI methods employed in this study are the same as those used in that study (Dugué et al., 2017a), but here, instead of analyzing TPJ activity, we analyzed activity in occipital areas.

481 **Participants**

482 Five participants (two male and three female, 24-30 years-old) participated in the study.
483 They all had normal or corrected-to-normal vision. The University Committee on Activities Involv-
484 ing Human Subjects at New York University approved the experimental protocol (IRB # 10-7094),
485 and participants provided written informed consent. Our study used single-participant ROI-based
486 analysis, and thus had a small sample size. The same sample size that has been used in many
487 fMRI studies in our labs (e.g. Dugué et al., 2017a; Herrmann et al., 2010; Liu et al., 2005; Liu et
488 al., 2006; Liu et al., 2007a; Pestilli et al., 2011; Freeman et al., 2013; Wang et al., 2014; Brouwer
489 et al., 2015), as well as in other labs (e.g. McMains and Somers, 2004; Moerel et al., 2016;
490 Mackey et al., 2017; Poltoratski et al., 2017; Bloem and Ling, 2019). Each participant performed
491 nine scanning sessions: one session to obtain a set of three high-resolution anatomical volumes,
492 two sessions for retinotopic mapping, three sessions for the exogenous attention condition and
493 three sessions for the endogenous attention condition (with the order counterbalanced among
494 participants). Participants performed several practice sessions outside the scanner prior to the
495 first scanning session of each attention condition.

496 **Stimuli**

497 Stimuli were generated on a Macintosh computer using the MGL toolbox (Gardner et al.,
498 2018b) in MATLAB (MathWorks). Stimuli were presented on a flat-panel display (NEC, LC-
499 XG250 MultiSync LCD 2110; refresh rate: 60 Hz; resolution: 1024 x 768 pixels) positioned at the
500 rear of the scanner bore and housed in a Faraday box with an electrically conductive glass front.
501 The display, calibrated and gamma corrected using a linearized lookup table, was at a viewing
502 distance of 172 cm from the participant, and visible through an angled mirror attached to the head
503 coil. A central, white fixation cross (0.3°) was presented throughout the experiment. The two stim-
504 uli were two 4-cpd gratings windowed by raised cosines (3° of diameter; 7% contrast), one in
505 each bottom quadrant (5° horizontal eccentricity; –2.65° altitude). Both endogenous cues and
506 exogenous cues were white rectangles (0.7°). The endogenous cues appeared adjacent to the
507 fixation cross indicating one of the two lower quadrants (0.35° horizontal eccentricity from the
508 edge of the fixation cross, and 0.35° altitude). The exogenous cues appeared adjacent to an

upcoming grating stimulus, vertically aligned with the stimulus and above the horizontal meridian (1° away from the edge of the grating stimulus; and the edge of the cue 4.44° horizontal eccentricity from the edge of the fixation cross).

Behavioral procedure

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

In both exogenous and endogenous condition, cues were presented for 67 ms, indicating either the bottom left or right quadrant of the screen. The inter-stimulus interval (ISI) between 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. Kinchla et al., 1995; Carrasco and Yeshurun, 1998; Liu et al., 2005; Pestilli et al., 2011). 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 (Nakayama and Mackeben, 1989; Mackeben and Nakayama, 1993; Liu et al., 2007b; Müller, 2014).

The behavioral effects of endogenous attention are sustained (e.g. Ling and Carrasco, 2006c) and thus, as shown in ERP studies (e.g. Seiss et al., 2009), 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 Carrasco 2011). 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. Kinchla et al., 1995; Carrasco and Yeshurun, 1998; Liu et al., 2005; Pestilli et al., 2011). 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; Phillips, 1974). 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 notice that cue validity does not affect cueing effectiveness for exogenous attention, although it does so do endogenous attention (e.g. Sperling and Melchner, 1978; Kinchla, 1980; Giordano et al., 2009).

Endogenous and exogenous attention conditions were performed in separate sessions to ensure optimal manipulation of each attention system. Participants first performed two practice sessions outside the scanner before the first session of each attentional scanning condition. To equate task difficulty for both attention conditions, using a staircase procedure, the tilt of the target grating was adjusted for each participant to achieve ~80% correct performance in the valid trials in each attention condition. In each of the six experimental scanning sessions (three

564 sessions of exogenous attention and three of endogenous), participants performed 14 runs of 40
565 trials each, as well as a run of stimulus localizer (see MRI procedure). The tilt was then adjusted
566 between runs to maintain overall performance at ~80% correct.

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

573 **MRI Procedure**

574 *Scanning.* Imaging was conducted on a 3T Siemens Allegra head-only scanner (Erlan-
575 gen, Germany), using a Siemens NM-011 head coil (to transmit and receive) to acquire anatom-
576 ical images, a receive-only 8-channel surface coil array (Nova Medical, Wilmington, MA) to ac-
577 quire functional images. To minimize participants' head movements, padding was used.

578 For each participant, three high-resolution anatomic images were acquired in one scan-
579 ning session, using a T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) se-
580 quence (FOV = 256 x 256 mm; 176 sagittal slices; 1 x 1 x 1 mm voxels), and were co-registered
581 and averaged. Using FreeSurfer (public domain software; http://surfer.nmr.mgh.harvard.edu),
582 the gray matter was segmented from these averaged anatomical volumes. All subsequent anal-
583 yses were constrained only to voxels that intersected gray matter.

584 T2*-weighted echo-planar imaging sequence (i.e. functional images; TR = 1750 ms; TE
585 = 30 ms; flip angle = 90°) measured blood oxygen level-dependent (BOLD) changes in image
586 intensity (Ogawa et al., 1990). In each volume, 28 slices covered the occipital and posterior pa-
587 rietal lobes and were oriented 45° to the calcarine sulcus (FOV = 192 x 192 mm; resolution = 2
588 x 2 x 2.5 mm; no gap). To align functional images from different sessions to the same high-reso-
589 lution anatomical volume for each participant, we acquired an additional T1-weighted anatomical
590 images in the same slices as the functional images (spin echo; TR = 600 ms; TE = 9.1 ms;

flip angle = 90°; resolution = 1.5 × 1.5 × 3 mm) during each scanning session, and used them in a robust image registration algorithm.

MRI data pre-processing. Imaging data were analyzed in MATLAB, using mrTools (Gardner et al., 2018a) and custom software. To allow longitudinal magnetization to reach steady state, the first eight volumes of each run were discarded. Spatial distortion was corrected using the B0 static magnetic field measurements performed in each session. The functional data were then motion corrected, the linear trend was removed, and a temporal high-pass filter was applied (cut-off: 0.01 Hz) to remove slow drifts and low-frequency noise in the fMRI signal.

Retinotopic mapping. We followed well-established conventional traveling-wave, phase-encoded methods. Using clockwise and counter-clockwise rotating checkerboard wedges, we measured phase maps of polar angle. Using contracting and expending checkerboard rings, we measured eccentricity maps (Engel et al., 1994; Sereno et al., 1995; Engel et al., 1997; Larsson and Heeger, 2006; Wandell et al., 2007). **Figure 2** (left panel) shows the visual areas that were drawn by hand on flattened surface of the brain, following published conventions (Engel et al., 1997; Larsson and Heeger, 2006; Wandell et al., 2007; Liu et al., 2007a).

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 (Kay et al., 2013a), 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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