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

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ABSTRACT

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), for pre- or post-cueing in endogenous and exogenous conditions, while observers performed the same task. We found stronger modulation in contralateral than ipsilateral visual regions to the attended hemifield, and higher activity in the valid- than invalid-trials. For endogenous, modulation of stimulus-evoked activity due to a pre-cue increased along the visual hierarchy, but was constant due to a post-cue. In contrast, for exogenous, 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 visual areas during orienting and reorienting of attention; endogenous facilitates both the encoding and the readout of visual information whereas exogenous only facilitates the encoding of information.

Keywords: exogenous attention, endogenous attention, fMRI activity, striate and extra-striate 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. 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 has 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 (Busse et al., 2008; Wang et al., 2015) and fMRI (Mayer et al., 2004; Peelen et al., 2004; Liu et al., 2005; Kincade et al., 2005; Natale et al., 2006; Müller and Kleinschmidt, 2007; Esterman et al., 2008; Müller and Ebeling, 2008; Heinen et al., 2011; Mulckhuyse et al., 2011) studies.

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 observers 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, to overt attention or to 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 striate and extra-striate visual 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	X	RT	Group-averaged	**Occipital:** *Cuneus, MOG, SOG* + Frontal Temporo-Parietal	No	No
	SOA=100 or 800 ms							
Peelen et al., 2004	central arrow 75% valid	brightening of pe-ripheral placeholder 50% valid	square	RT	Group-averaged	**Occipital:** *Cuneus* + Frontal Temporo-Parietal	No	No
	SOA=550 ms							
Natale et al., 2006	single peripheral rectangular frame 100% valid	five peripheral rec-tangular frames 20% valid	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
	SOA=8, 8.15, 8.3, 8.45 or 8.6 s							
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	T vs. L	RT (% correct)	Group-averaged	**Occipital:** *LO, MT, Cuneus, Fusiform, SOG* + Frontal Temporo-Parietal	No	No
	SOA=2160 ms							
Esterman et al., 2008	color change of a peripheral place-holder 75% valid	50% valid	face identity	RT (% correct)	ROI-based (FFA) + Group-averaged	**Occipital:** *FFA* + Frontal Temporo-Parietal	Yes	No
	SOA=300 ms							
Current study	central bar 75% invalid SOA=310 ms	peripheral bar 50% valid SOA=110 ms	orientation	d-prime (RT)	ROI-based	**Occipital:** *V1, V2, V3, V3A, hV4, LO1*	Yes	Yes
Studies NOT including Occipital areas								
Detection tasks								
Rosen et al., 1999	central arrow 80% valid	peripheral dot 50% valid	filling of a square	RT	Group-averaged	Frontal Temporo-Parietal	No	No
	SOA=400, 550 or 700 ms							

Discrimination tasks								
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.*

Here, with the same participants, task, stimuli and task difficulty for all attention manipulations, we tested the following four predictions: (1) Pre-cueing should induce an attentional modulation of fMRI activity, higher in the valid than the invalid condition in which attention needs to be reoriented to the opposite location to perform the task (e.g., Liu et al., 2005). (2) Both endogenous and exogenous pre- and post-cueing effects should be stronger in contralateral than ipsilateral visual regions relative to the attended hemifield (e.g., Liu et al., 2005; Serences and Yantis 2007; Pestilli et al., 2011). (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; Kastner et al., 1999; Pestilli et al., 2011; for reviews Chica et al., 2013; Beck and Kastner, 2014). 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, given the increased distance from the source. (4) Post-cueing endogenous (Nobre et al., 2004b; Hulme et al., 2009; Pestilli et al., 2011; Sergent et al., 2011), but not exogenous (Liu et al., 2005), attention should induce attentional modulation of fMRI activity in early visual areas. Voluntary, endogenous attention would facilitate reading out perceptual information (Dugué et al., 2017a), and modulate its processing (Nobre et al., 2004a; Hulme et al., 2009; Pestilli et al., 2011; Sergent et al., 2011). The only fMRI study assessing the effects of post-cueing exogenous attention found no attentional modulation of fMRI activity in early visual areas (Liu et al., 2005); some behavioral studies report post-cueing effects (Sergent et al., 2013; Thibault et al., 2016)) but others found no such effects (Carrasco and Yeshurun, 1998; Gobell and Carrasco, 2005).

To test these four predictions, we measured fMRI activity and compared the effects of endogenous and exogenous attention in early visual areas while the same observers performed the same task –a 2-AFC orientation discrimination task, contingent upon contrast sensitivity (Nachmias, 1967; Carrasco et al., 2000; Pestilli et al., 2009). We used a fully-crossed design: two attention conditions –endogenous or exogenous attentional orienting– and two types of cueing –pre- or post-cue. We evaluated fMRI activity at both the attended and the un-attended locations, given the ubiquitous performance tradeoffs at attended (benefits) and unattended (costs)

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

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

197

198 **RESULTS**

199 **Endogenous and exogenous attention improve performance**

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

205 We calculated performance accuracy (d') in each condition as the main dependent varia-
206 ble, for each observer separately (**Figure 1B**, top row). We conducted a three-way repeated
207 measures 2x2x2 ANOVA (exogenous/endogenous x valid/invalid x pre/post-cue). There was bet-
208 ter performance for valid than invalid cues ($F(1,4)=23.6$, $p=0.008$). Exogenous versus endoge-
209 nous cues were statistically indistinguishable ($F(1,4)<1$), and there was no evidence for a

difference between pre- versus post-cues (F(1,4)<1). None of the two or three-way interactions were significant.

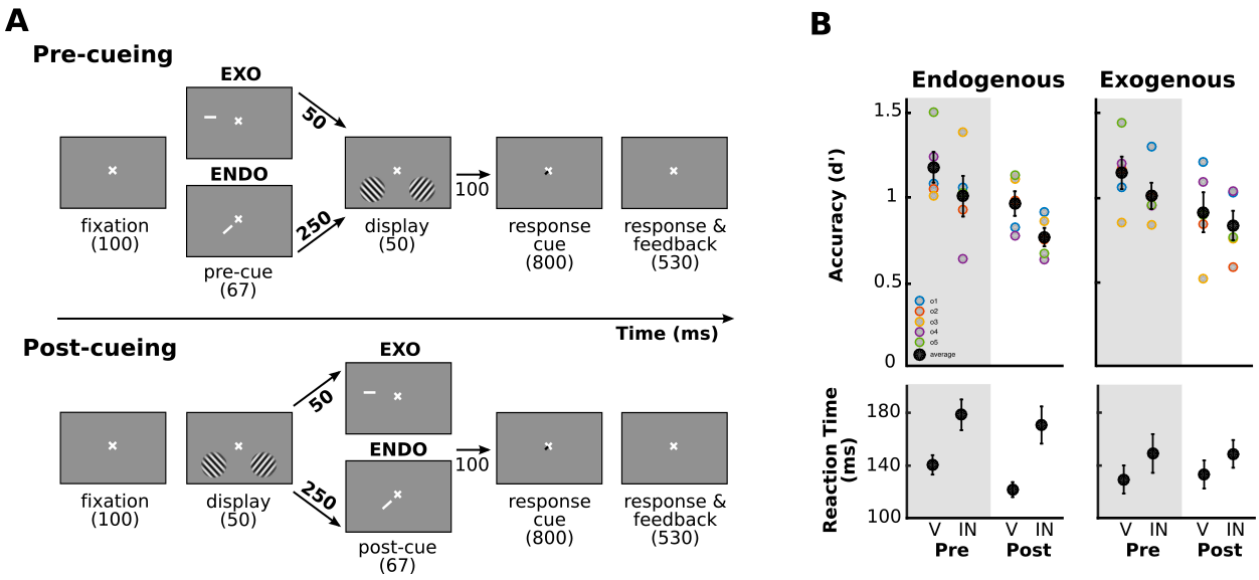

Figure 1. Experimental protocol. A. *Observers performed a 2-AFC orientation-discrimination task. Pre-cues were presented before the gratings. Post-cues were presented after the gratings. Exogenous cues appeared in the periphery, above one of the two grating locations. Endogenous cues appeared at the center of the screen and pointed toward one of the two grating locations (The display is not at scale for the purpose of visibility). The ISI between the cue and the gratings differed between exogenous (50 ms) and endogenous (250 ms) conditions. A response cue indicated the target location and instructed observers to press one of two keys to indicate whether the target grating was tilted clockwise or counterclockwise of vertical. The fixation-cross turned green for a correct answer, and red for an incorrect answer.* ***B.*** *Behavioral performance for each observer (n=5) and averaged across them. (Top) Performance accuracy (d') as a function of cueing condition. (Bottom) Median reaction time. V, valid cue (location of pre-cue/post-cue and response cue matched). IN, invalid cue (location of pre-cue/post-cue and response cue mismatched). Pre, pre-cue presented before the grating stimuli. Post, post-cue presented after gratings. Valid cues led to more accurate and faster responses; there was no evidence for a speed-accuracy trade-off. Error bars, ± 1 SEM across observers.*

Reaction time was also calculated in each condition, for each observer separately (**Figure 1B**, bottom row). The corresponding three-way ANOVA revealed that reaction times were faster for valid than invalid cues (F(1,4)=62.3, p=0.001). There was no evidence for a difference between exogenous and endogenous cues (F(1,4)=2.7, p=0.17), either for pre-cues or post-cues (F(1,4)=1.7, p=0.27). There were two significant interactions, indicating that the differences between pre-cues and post-cues (F(1,4)=8.1, p=0.047) and between valid cues and invalid cues (F(1,4)=16.2, p=0.02) were more pronounced for endogenous 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 (both accuracy 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**), 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 as a function of the contralateral and ipsilateral brain activity 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.

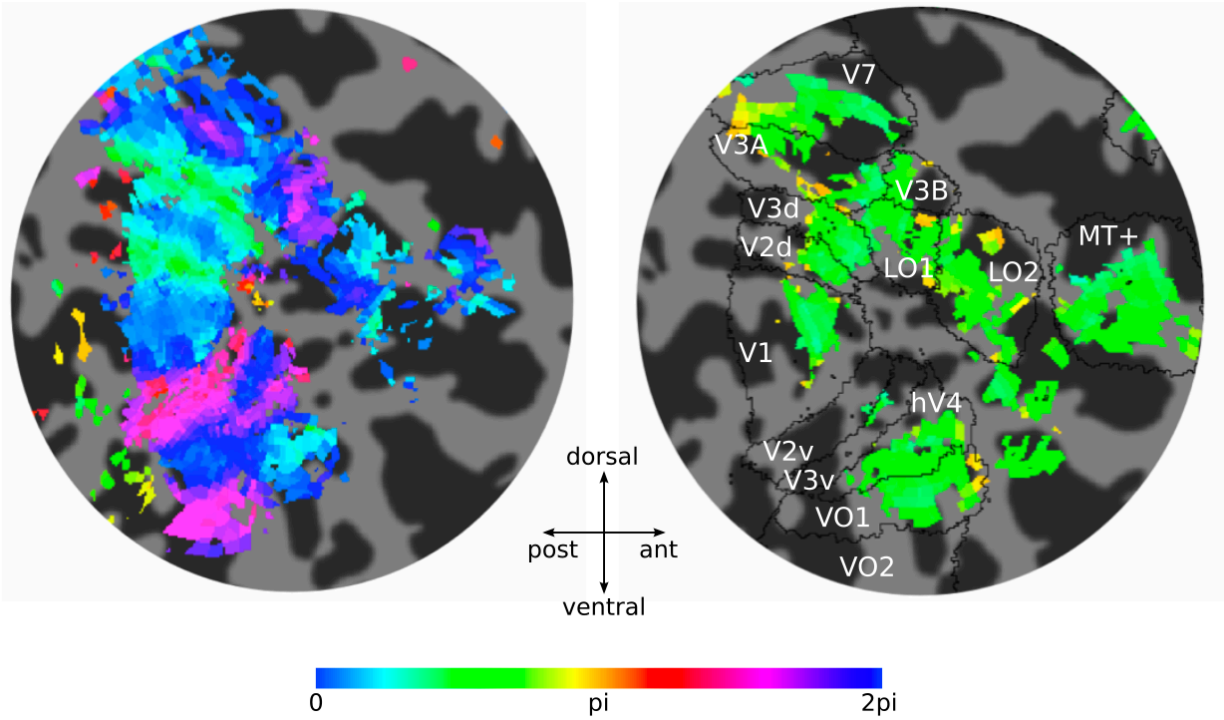

Figure 2. Retinotopic mapping and stimulus localizer of a representative observer. *A flattened representation of the right hemisphere occipital pole. Left, map of polar angle. The color of each voxel in the map represents the response phase of the time series in response to a rotating wedge stimulus. Right, stimulus localizer. The black outlines correspond to the retinotopic areas (defined for each observer based on their polar angle maps). The color of each voxel indicated 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 observers, 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 ($t(4) = 4.0$, $p = 0.01$). This was the case for each observer (**Figure 3B**). Together, these results are consistent with previous findings showing that fMRI response correlates with behavioral variability, and that attentional orienting increases fMRI signal in early visual cortex (for review Beck and Kastner, 2014).

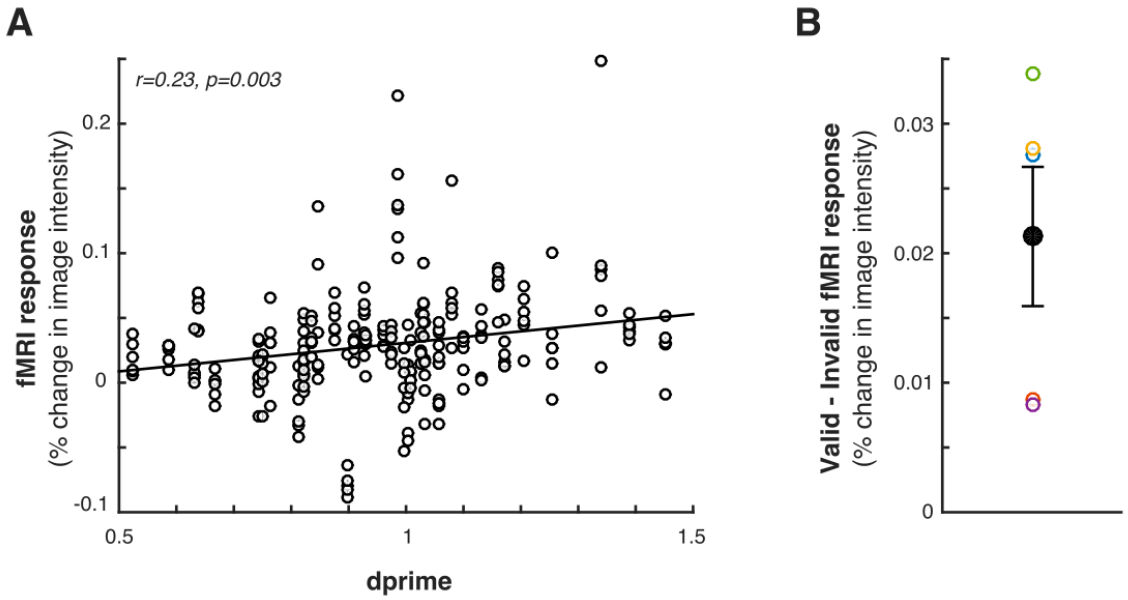

Figure 3. Inter-individual fMRI response. A. *Positive correlation between fMRI response and behavioral performance (Pearson correlation r = 0.23, p = 0.003). Each dot indicates fMRI response amplitude measured from one ROI and one observer, separately for each attentional condition (pre and post-cue, valid and invalid).* ***B.*** *fMRI response difference between valid and invalid trials combined across all conditions and ROIs for each observer (colored dots), and across observers (black dot; average significantly positive: t(4) = 4.0, p = 0.01). Error bar, ± 1 SEM across observers.*

We then tested our two novel predictions: (1) attentional modulation of fMRI stimulus-evoked activity increases along the visual hierarchy for endogenous, but is constant for exogenous, pre-cueing; and (2) attentional modulation of fMRI stimulus-evoked activity for endogenous 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, endogenous post-cueing or exogenous post-cueing conditions ($p > .1$).

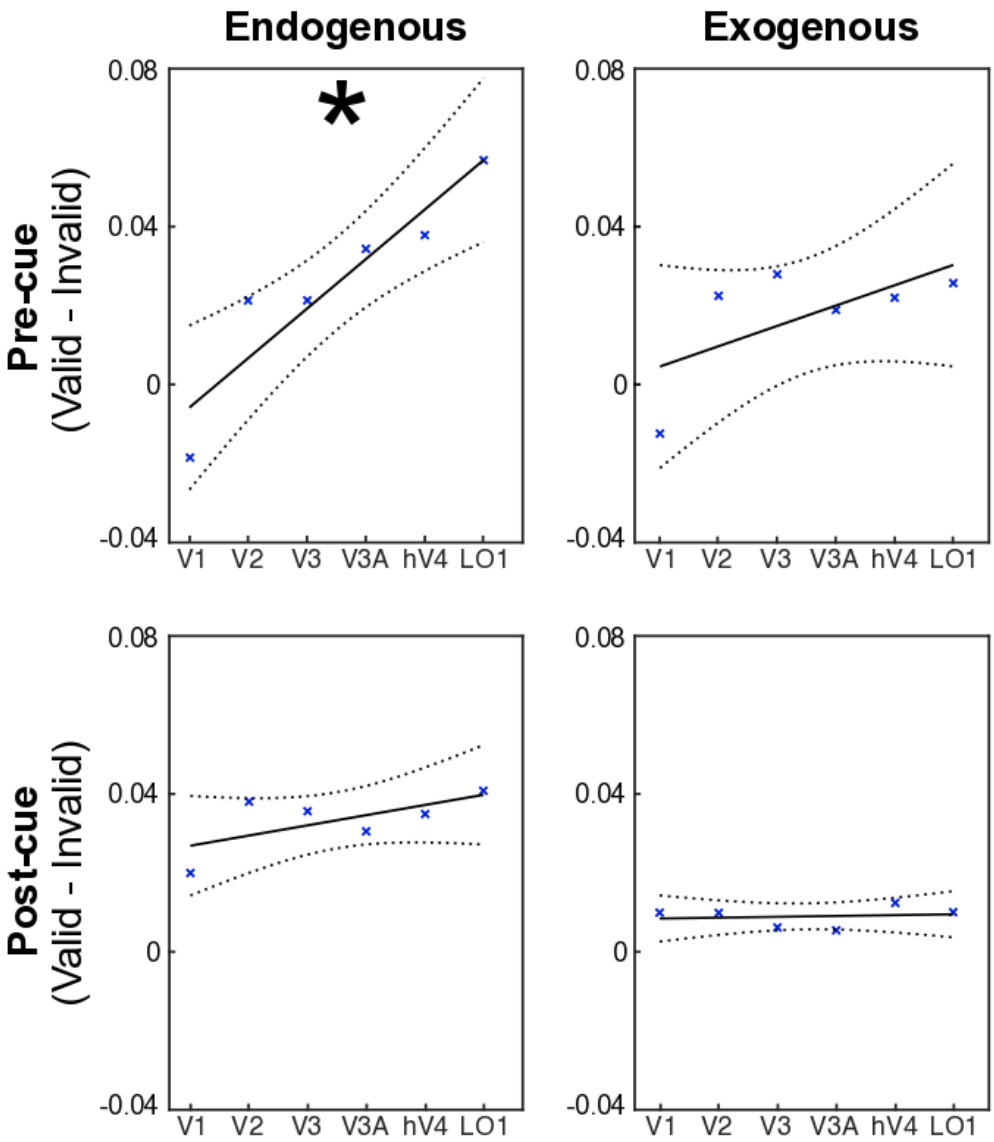

Figure 4. Specificity of pre and post-cueing for endogenous and exogenous attention. *The difference in fMRI response between valid and invalid is plotted separately for pre- and post-cue conditions for each ROI. *, Statistically significant difference between valid and invalid, separately for pre and post-cueing (p < 0.05). Error bars on plots are ± 1 SEM.*

For both endogenous ($p < 0.05$ for V3a, V4 and LO1; trend ($p = 0.077$) for V3; t-tests) and exogenous ($p < 0.05$ for V3, V3A, hV4 and LO1; trend ($p = 0.074$) for V2; t-tests) attention 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 ($p = 0.079$) 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. Taken together, these results confirm both of our predictions.

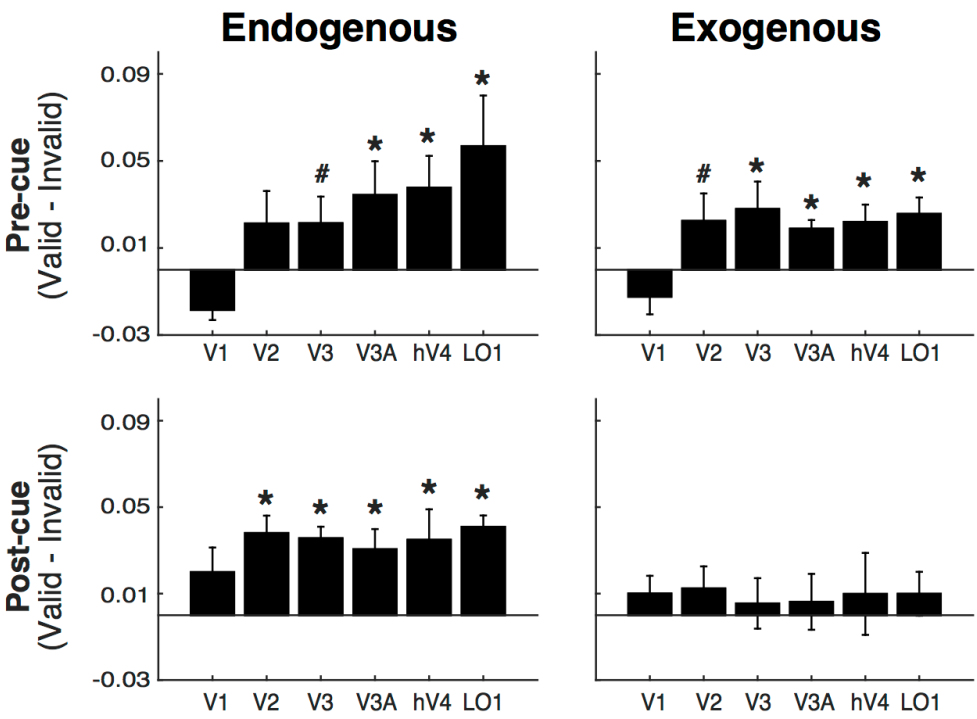

Figure 5. Single ROI responses for pre and post-cueing and for both endogenous and exogenous attention. *The difference in fMRI response between valid and invalid is plotted separately for pre and post-cue conditions for each ROI. *, Statistically significant difference between valid and invalid, separately 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. ANOVAs conducted separately for each ROI revealed a main effect of validity, i.e. higher activity for valid than invalid cued locations in all visual areas (p<0.05; t-tests), except V1.

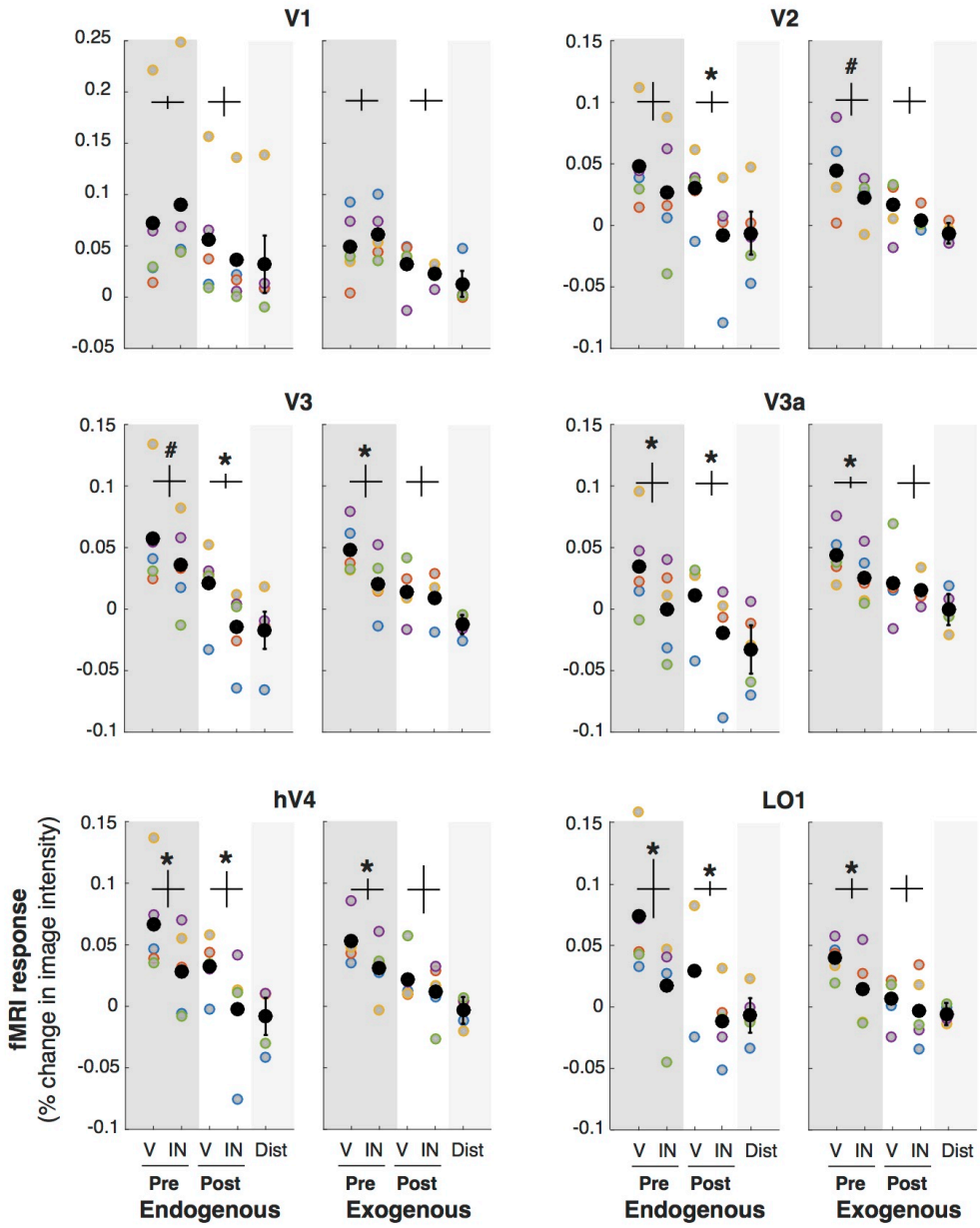

Figure 6. Specificity of each visual ROI for endogenous and exogenous attention. *fMRI response amplitude was measured for each attentional condition. V: valid cue condition (target location matches the location indicated by pre-cue/post-cue). IN: invalid cue condition (target location at the opposite 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. Dist: all conditions averaged in the ipsilateral ROI. Each colored point corresponds to the data of one observer. The black points represent the average across all 5 observers. *, Statistically significant difference between valid and invalid, separately for pre and post-cueing ($p < 0.05$). #, trend ($p < 0.1$). Error bars are plotted on the difference between valid and invalid and represent ± 1 SEM across observers.*

335 **DISCUSSION**

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

342 Previous studies comparing endogenous and exogenous attention conditions state vari-
343 ous attentional effects in early visual areas (see **Table 1**). Some report differential effects be-
344 tween these attention conditions in the right LO and MT (Kincade et al., 2005), others in the
345 cuneus (Peelen et al., 2004; Mayer et al., 2004; Kincade et al., 2005), the occipital gyrus (SOG,
346 MOG, LOG; Mayer et al., 2004; Kincade et al., 2005; Natale et al., 2006), the fusiform area (Kin-
347 cade et al., 2005; Natale et al., 2006; Esterman et al., 2008), and the TOS, LG and SC (Natale
348 et al., 2006). This lack of clear picture regarding the differential impact of endogenous and exog-
349 enous spatial attention is likely due to the methodological differences and limitations we dis-
350 cussed in the Introduction (see also **Table 1**). In any case, it is often assumed that the effects of
351 endogenous and exogenous attention are the same in striate and extra-striate areas (Corbetta
352 and Shulman, 2002; Peelen et al., 2004; Corbetta et al., 2008; Chica et al., 2013; Beck and
353 Kastner, 2014).

354 To further our knowledge of the neural correlates of attention, we investigated both atten-
355 tional orienting (valid cueing) and reorienting (invalid cueing), critical in an ever-changing envi-
356 ronment (Dugué et al., 2016; 2017b; Senoussi et al., 2019). Furthermore, given ubiquitous per-
357 formance tradeoffs between attended (benefits) and unattended (costs) locations (e.g. Pestilli
358 and Carrasco, 2005; Giordano et al., 2009; Montagna et al., 2009; Herrmann et al., 2010), we
359 assessed activity at both attended (contralateral ROI) and unattended (ipsilateral ROI) locations.
360 Finally, we investigated how attentional effects varied as a function of pre- and post-cueing, thus
361 contrasting the neural correlates of perceptual and post-perceptual processing of information.

362 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). 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).

In the endogenous attention condition, there was an increase in attentional modulation of stimulus-evoked activity along the hierarchy of visual areas. 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 to weakening the effect of attention in V1. The accrual time in the current endogenous condition was relatively short (1300 ms in the valid condition and 500 ms in the invalid condition) compared to previous studies investigating endogenous, voluntary attention, in which the cue and/or stimuli were presented for a long duration to maximize BOLD measurements (e.g. Boynton et al., 1999; Brefczynski and DeYoe, 1999; Somers et al., 1999; Pestilli et al., 2011). We chose the minimum SOA (317 ms) at which performance benefits plateau to have as comparable conditions as

possible to the accrual time with the SOA for exogenous attention (117 ms). This short accrual time may have limited the effects of attentional feedback to V1.

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

Unlike in the endogenous pre-cueing condition in which the attention effect increased along the processing stream, for the endogenous post-cueing effect there was no evidence that it varied across these visual areas. The constant effect in the post-cue 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 (Kay et al., 2013b); (2) the top-down modulations from frontal and parietal areas feedback to visual cortex with diminishing effects in earlier visual areas (Chica and Lupiáñez, 2009; Kastner et al., 1999; Pestilli et al., 2011).

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), 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.

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, observers were attending to the same location throughout the trial, whereas for the latter, when the response cue did not match the pre-cue, observers 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 observers had been processing the target for almost 500 ms before the response cue appeared. When the response cue matched the pre-cue, observers 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 observers had to switch after 500 ms to the other location (ipsilateral) thus accumulating less activity. Similarly, the accumulation time for the invalid cue condition in exogenous attention was only about 300 ms. This accrual time explanation could also account for the larger difference between contralateral and ipsilateral for pre-cues than post-cues, i.e. there is a 300 ms accumulation when the exogenous pre-cue is invalid, while only 100 ms when the post-cue in invalid. Likewise, the larger modulatory effect for endogenous relative to exogenous attention is consistent with the difference in accrual time.

The results of the present study complement our recent study (Dugué et al., 2017a) in which we demonstrated that sub-regions of the Temporo-Parietal Junction (TPJ) that respond specifically to visual stimuli are more active when attention needs to be spatially reoriented (invalid cueing) than when attention remains at the cued location (valid cueing), and that partially overlapping specific visual sub-regions mediate reorienting after orienting of endogenous or exogenous attention. 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 methods employed in this study as well as their description are identical to 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). We used optimal spatial and temporal parameters to maximize the effects of these two types of attention, i.e. the benefits at the attended location and costs at the unattended location, on an orientation discrimination task. The same observers performed the same discrimination task under endogenous and exogenous attention to enable direct comparison between these conditions (reviews by Carrasco, 2011; Carrasco and Barbot, 2015).

Observers

Five observers (three female, 24-30 years-old) with normal or corrected-to-normal vision participated in the study. Observers provided written informed consent. The University Committee on Activities Involving Human Subjects at New York University approved the experimental protocol. Each observer participated in 10 scanning sessions: one session to obtain a set of three high-resolution anatomical volumes, two sessions for retinotopic mapping, three sessions for the exogenous attention condition and three sessions for the endogenous attention condition (order

counterbalanced between observers). Prior to the first scanning session of each attention condition, observers performed several practice sessions outside the scanner.

Stimuli

Stimuli were generated using MATLAB (MathWorks) and the MGL toolbox (Gardner et al., 2018b) on a Macintosh computer. Stimuli were displayed on a flat-panel display (NEC, LC-XG250 MultiSync LCD 2110; resolution: 1024 x 768 pixels; refresh rate: 60 Hz) housed in a Faraday box with an electrically conductive glass front, positioned at the rear of the scanner bore. Observers viewed the display through an angled mirror attached to the head coil, at a viewing distance of 172 cm. The display was calibrated and gamma corrected using a linearized lookup table. A white fixation cross (0.3°) was present at the center of the screen throughout the experiment. The stimuli consisted of two gratings (4 cpd) windowed by raised cosines (3° of diameter; 7% contrast). The stimuli were presented in the bottom quadrants (5° horizontal eccentricity; –2.65° altitude). Endogenous cues were white rectangles (0.7°), positioned adjacent to the fixation cross indicating one of the two lower quadrants (0.35° horizontal eccentricity from the edge of the fixation cross, and 0.35° altitude). Exogenous cues were also white rectangles (0.7°), but were positioned adjacent to an upcoming grating stimulus, 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) and vertically aligned with the stimulus.

Behavioral procedure

A single trial lasted 1700 ms for the exogenous attention condition and 1900 ms for the endogenous attention condition, the only difference being the SOA between the cue and the display; the timing of all the visual stimuli was the same in both attention conditions (**Figure 1**; note that for illustration purposes, the display is not at scale). In 40% of the trials (pre-cue condition), a cue was shown first, followed by the pair of gratings. In 40% of the trials (post-cue condition), the order of presentation of the cue and the gratings was reversed. In 10% of the trials, the gratings were not presented ('cue-only' trials). In the remaining 10% of the trials, neither a cue nor the gratings were presented ('blank' trials). 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, observers were instructed to report the orientation of a target grating, i.e., clockwise or counter-clockwise compared to vertical, by pressing one of two keys. For cue-only and blank trials, observers were asked to press a third key.

Cues (both exogenous and endogenous) were presented for 67 ms, indicating either the left or the right grating location. The inter-stimulus interval (ISI) between the pre-cues and the gratings was 50 ms for exogenous cues and 250 ms for endogenous cues, resulting in stimulus-onset asynchronies (SOA) of 117 ms and 317 ms, optimal delays to manipulate exogenous and endogenous attention respectively and maximize their behavioral consequences (Nakayama and Mackeben, 1989; Mackeben and Nakayama, 1993; Liu et al., 2007b; Müller, 2014), while keeping the trial duration as similar as possible. The behavioral effects of endogenous attention are sustained (e.g. (Ling and Carrasco, 2006c)) and can thus still be present in later brain activity, as shown in ERP studies (e.g. (Seiss et al., 2009)). Further, the brain responses elicited by exogenous and endogenous cues are different during 300 ms following cue onset. The gratings were shown for 50 ms. For the post-cue trials we used the same timings but inverted the order of presentation, so that the cues followed the stimuli (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 indicated which of the two gratings was the target (50% of the trials at each location). Note that in all four trial conditions (exogenous/endogenous, pre-/post-cueing), the response cue appeared after both the cue and the stimuli had disappeared. The maximum delay between the stimuli offset and the response cue onset was brief (~400 ms max in the endogenous condition). This time interval is less than typically associated with a demand for working memory (>600 ms; Phillips, 1974). Visual feedback was provided immediately following each trial. The fixation cross turned green or red to indicate a correct or incorrect response, respectively. If observers had not pressed any key after 530 ms, the fixation cross did not change color indicating that they missed the response window.

Exogenous, peripheral cues were not informative regarding the target location or orientation; the cue and the target location matched in 50% of the trials (valid trials), but not in the other

529 50% of the trials (invalid). Endogenous, central cues were informative of the target location but
530 not its orientation; cues pointed towards the target in 75% of trials (valid trials), but not in the
531 remaining 25% of trials (invalid). Participants were informed of this validity. It is important to notice
532 that cue validity does not affect cueing effectiveness for exogenous attention, although it does so
533 do endogenous attention (e.g. Giordano et al., 2009). Finally, using a staircase procedure, per-
534 formance was equated between the two conditions.

535 Endogenous and exogenous attention conditions were performed in separate sessions to
536 ensure optimal manipulation of each attention system. Each of the 3 sessions of the exogenous
537 condition and 3 sessions of the endogenous consisted of 14 runs of 40 trials each, as well as an
538 additional run of stimulus localizer (see MRI procedure). Prior to the first session of each atten-
539 tional scanning condition, observers performed two practice sessions outside the scanner. The
540 tilt of the grating was adjusted so that each observer would achieve ~80% correct performance
541 in the valid trials. During the scanning sessions, the tilt was adjusted between runs to maintain
542 this overall performance level. Eye position was monitored using an infrared video camera sys-
543 tem (Eyelink 1K, SR Research, Ottawa, Ontario, http://www.sr-research.com/EL_1000.html).
544 Trials in which the observers blinked or broke fixation (1.5° away from fixation) at any point during
545 the trial sequence (from fixation onset to response cue offset; 13% ± 4% of the trials on average
546 across all observers) were identified and removed from the behavioral analysis (see Results),
547 and regressed separately in the MRI analysis (see below).

548 **MRI Procedure**

549 *MRI scanning.* Imaging was conducted on a 3T Siemens Allegra head-only scanner (Er-
550 langen, Germany). Padding was used to minimize observers' head movements. Anatomical im-
551 ages were acquired using a Siemens NM-011 head coil to transmit and receive. In a single scan-
552 ning session for each observer, three high-resolution anatomic images were acquired using a
553 T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) sequence (FOV = 256 x
554 256 mm; 176 sagittal slices; 1 x 1 x 1 mm voxels). These three images were co-registered and
555 averaged. We then used the public domain software FreeSurfer

556 (http://surfer.nmr.mgh.harvard.edu), to segment the gray matter from these averaged anatomical
557 volumes. All subsequent analyses were constrained only to voxels that intersected gray matter.

558 Functional images were acquired with a receive-only 8-channel surface coil array (Nova
559 Medical, Wilmington, MA). T2*-weighted echo-planar imaging sequence (TR = 1750 ms; TE = 30
560 ms; flip angle = 90°) measured blood oxygen level-dependent (BOLD) changes in image intensity
561 (Ogawa et al., 1990). One volume contained 28 slices oriented 45° to the calcarine sulcus and
562 covered the occipital and posterior parietal lobes (FOV = 192 x 192 mm; resolution = 2 x 2 x
563 2.5 mm; no gap). In each session, we acquired T1-weighted anatomical images in the same
564 slices as the functional images (spin echo; TR = 600 ms; TE = 9.1 ms; flip angle = 90°; resolution
565 = 1.5 × 1.5 × 3 mm). The in-plane images were used to align functional images from different
566 sessions to the same high-resolution anatomical volume for each participant, using a robust im-
567 age registration algorithm.

568 *Pre-processing of the MRI data.* Imaging data were analyzed using mrTools (Gardner et
569 al., 2018a) and custom software written in MATLAB. The first eight volumes of each run were
570 discarded to allow longitudinal magnetization to reach steady state. The measurements of the
571 B0 static magnetic field performed in each session were used to correct for spatial distortion. Pre-
572 processing of the functional data included motion correction, linear trend removal, and tem-
573 poral high-pass filtering (cutoff: 0.01 Hz) to remove low-frequency noise and slow drifts in the
574 fMRI signal.

575 *Retinotopic mapping.* Retinotopic mapping procedures followed well-established methods
576 using conventional traveling-wave, phase-encoded methods. Phase maps of polar angle were
577 measured using clockwise and counter-clockwise rotating checkerboard wedges, and eccen-
578 tricity maps were measured using contracting and expending checkerboard rings (Engel et al.,
579 1994; Sereno et al., 1995; Engel et al., 1997; Larsson and Heeger, 2006; Wandell et al., 2007).
580 **Figure 2** (left panel) shows the borders of visual areas drawn by hand on flattened surface rep-
581 resentations of the brain following published conventions (Engel et al., 1997; Larsson and Hee-
582 ger, 2006; Wandell et al., 2007; Liu et al., 2007a).

Stimulus localizer. The stimuli were the same size, spatial frequency, and location as those in the main experiment, but they were at full contrast, and their orientation and phase were randomly changed every 200 ms to avoid adaptation. A localizer run consisted of a two-condition block alternation protocol: 16 cycles, each cycle was 17.5 s (8.75 s with the stimuli on, 8.75 s stimulus off). Observers completed one localizer run in each scanning session of the main experiment (6 runs overall, 4 min each). Observers were instructed to fixate a cross at the center of the screen throughout each run. Data were averaged across the 6 runs and analyzed using the same methods as for the retinotopic mapping scans, to define the cortical representation of the gratings. Each retinotopic ROI was further restricted to voxels that responded positively during the blocks when the grating stimuli were presented. A sinusoid was fit to the fMRI time series from each voxel. To be conservative, voxels were included in the ROI if the best-fit sinusoid had a phase value between 0 and pi, and if the correlation (technically, coherence) between the best-fit sinusoid and the time series was greater than 0.2 (**Figure 2**, right panel). In addition, we conducted the analysis without restricting the ROI to this coherence level, yielding similar results that supported the same conclusions.

Event-related analysis. fMRI time series in the main experiment 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). fMRI response amplitudes were then computed from the denoised data using linear regression, with twelve regressors: right and left valid pre-cue, right and left invalid pre-cue, right and left valid post-cue, right and left invalid post-cue, right and left cue-only, blank (no cue nor stimulus) and eye-movements (trials in which observers broke fixation or blinked). The resulting fMRI response amplitudes (for correct trials only) were then averaged across observers, separately for each ROI and separately for each hemisphere.

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