

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

3
4 Laura Dugué^{1,2,3,4,5}, Elisha P. Merriam^{1,2,6}, David J. Heeger^{1,2} & Marisa Carrasco^{1,2}

5
6
7
8
9
10 ¹ Department of Psychology, New York University

11 ² Center for Neural Science, New York University

12 ³ CNRS (Integrative Neuroscience and Cognition Center, UMR 8002) Paris, France

13 ⁴ Université de Paris, Paris, France

14 ⁵ Institut Universitaire de France (IUF), Paris, France

15 ⁶ Laboratory of Brain and Cognition, NIMH/NIH, Bethesda, MD

16

17

18 **Running title:** endogenous and exogenous attention

19

20

21 **Corresponding author:**

22 Laura Dugué

23 Current address: 45 rue des Saints-Pères 75006 Paris, FRANCE

24 laura.dugue@u-paris.fr

25 **ABSTRACT (148 words)**

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

38

39 **Keywords:** exogenous attention, endogenous attention, fMRI activity, occipital visual areas, top-
40 down and bottom-up processing, visual perception.

41 INTRODUCTION

42 Spatial, covert visual attention is the selective processing of visual information in space,
43 without change in gaze. Attention can be allocated voluntarily –endogenous attention– or invol-
44 untarily –exogenous attention. Endogenous and exogenous attention have different temporal dy-
45 namics; endogenous takes about 300 ms to be deployed and can be sustained at will whereas
46 exogenous attention takes only about 100 ms to be deployed and it is transient (for review see
47 Carrasco, 2011; Carrasco and Barbot, 2015). These two types of attention often have similar
48 perceptual consequences (reviews by Carrasco, 2011; Carrasco and Barbot, 2015), but notable
49 exceptions indicate that whereas endogenous attention acts in a flexible way, exogenous atten-
50 tion acts in an inflexible or automatic way. For instance: (a) The benefits and costs in perception
51 (discriminability and speed of information accrual) scale with cue validity for endogenous but not
52 for exogenous attention (e.g. Sperling and Melchner, 1978; Kinchla, 1980; Giordano et al., 2009);
53 (b) The effects of covert attention on contrast sensitivity often differ for endogenous and exoge-
54 nous attention (e.g. Doshier and Lu, 2000; Ling and Carrasco, 2006a; Pestilli et al., 2009; Barbot
55 et al., 2012); and (c) For a texture segmentation task in which heightened spatial resolution im-
56 proves or impairs performance as a function of target eccentricity, endogenous attention im-
57 proves performance across eccentricity, whereas exogenous attention improves performance at
58 peripheral locations where resolution is poor, but hampers performance where resolution is al-
59 ready high for the task at hand (e.g. Yeshurun and Carrasco, 1998; Carrasco et al., 2006; Ye-
60 shurun et al., 2008; Barbot and Carrasco, 2017; Jigo and Carrasco, 2018).

61 Basic visual processes, such as contrast sensitivity and spatial resolution, are mediated
62 by activity in early visual cortex, and are altered by covert attention (reviews by Carrasco and
63 Yeshurun, 2009; Carrasco, 2011; Anton-Erxleben and Carrasco, 2013; Carrasco and Barbot,
64 2015). Specifically, single-unit studies in monkeys have demonstrated effects of endogenous
65 attention in occipital areas (e.g. McAdams and Maunsell, 1999; Reynolds et al., 2000; Martínez-
66 Trujillo and Treue, 2002; Williford and Maunsell, 2006; Mitchell et al., 2009; Reynolds and Hee-
67 ger, 2009; Ruff and Cohen, 2014; Luo and Maunsell, 2015). Additionally, fMRI studies have
68 shown that endogenous attention causes a baseline shift in early visual areas (e.g. Kastner et

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

75 Since Corbetta and Schulman's seminal review (2002) on the neural bases of endoge-
76 nous and exogenous attention, there has been emphasis on characterizing networks of brain
77 regions within the frontal and parietal lobes (for reviews see Chica et al., 2013; Beck and Kastner,
78 2014). Yet, there remains considerable debate regarding the dissociation between dorsal re-
79 gions, for endogenous attention, and ventral regions, for exogenous attention (e.g. Hahn et al.,
80 2006; Bowling et al., 2019), including the role of the temporo-parietal junction (TPJ; Doricchi et
81 al., 2010; Geng and Vossel, 2013; Silvetti et al., 2015; Dugué et al., 2017a). Classically, research-
82 ers have described endogenous attention as a top-down process, and exogenous attention as a
83 bottom-up process (e.g., Posner et al., 1980; Nakayama and Mackeben, 1989; Corbetta and
84 Shulman, 2002; Hahn et al., 2006; Beck and Kastner, 2009; Carrasco, 2011; Chica et al., 2013;
85 Beck and Kastner, 2014; Bowling et al., 2019). This characterization originated in psychophysics
86 experiments, and was then studied using fMRI, in which the two types of attention have been
87 often investigated separately (for reviews Beck and Kastner, 2009; Carrasco, 2011; Chica et al.,
88 2013; Beck and Kastner, 2014).

89 Studies of endogenous and exogenous attention focusing on parietal and frontal areas
90 have shown that the two types of attention differentially modulate fronto-parietal connectivity
91 (Buschman and Miller, 2009; Bowling et al., 2019). For example, there are critical differences in
92 the temporal order of neural responses in frontal and parietal cortex in monkeys between these
93 attention conditions, i.e. frontal activity precedes parietal activity during endogenous attentional
94 orienting, whereas parietal activity precedes frontal activity during exogenous orienting. Critically,
95 it is often assumed that the effects of endogenous and exogenous attention are the same in

96 striate and extra-striate areas (Corbetta and Shulman, 2002; Peelen et al., 2004; Corbetta et al.,
97 2008; Chica et al., 2013; Beck and Kastner, 2014).

98 A number of important considerations limit the conclusions that may be drawn from the
99 few studies that have directly compared independent effects of visual exogenous and endoge-
100 nous spatial attention (see **Table 1**):

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

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

110 (3) In the studies in which accuracy was not assessed (Rosen et al., 1999; Mayer et al., 2004;
111 Peelen et al., 2004; Natale et al., 2006), it is not possible to know whether task difficulty
112 was the same for both types of attention, and task difficulty can interact with the strength
113 of fMRI activity (Culham et al., 2001; Herath et al., 2001).

114 (4) For the studies in which eye position was not monitored while participants performed the
115 task in the scanner (Kim et al., 1999; Rosen et al., 1999; Mayer et al., 2004; Peelen et al.,
116 2004; Kincade et al., 2005; Natale et al., 2006; Meyer et al., 2018; Bowling et al., 2019),
117 the results could be due to covert attention, overt attention or both (Carrasco et al., 1995;
118 Beauchamp et al., 2001; Carrasco, 2011).

119 (5) Given that exogenous attention is a fast, transient process (for review see Carrasco, 2011;
120 Carrasco and Barbot, 2015), it was inappropriately manipulated in the studies in which
121 long stimulus onset asynchronies (SOA) were used (Rosen et al., 1999; Peelen et al.,
122 2004; Kincade et al., 2005; Natale et al., 2006; Esterman et al., 2008) making the com-
123 parison between the two attention conditions problematic.

124 (6) Except for two studies, one interested in attentional modulation in the Fusiform Face Area
125 (FFA; Esterman et al., 2008) and the other in the TPJ (Dugué et al., 2017), statistical
126 parametric mapping was applied to group averaged data to identify regions of the brain
127 that were active during task performance. Some found significant activity in the occipital
128 pole (Mayer et al., 2004; Peelen et al., 2004; Kincade et al., 2005; Natale et al., 2006),
129 but attentional modulation of fMRI activity was not systematically assessed across differ-
130 ent visual areas.

131 Given all these methodological limitations, it is unknown how these two types of attention
132 affect neural activity in each individual visuo-occipital areas, and how modulation of activity in
133 visual cortex is linked to changes in perceptual performance. (See Dugué and colleagues (Dugué
134 et al., 2017a), who published a table summarizing these and other methodological problems for
135 studies regarding covert attention and TPJ activation).

136 Typically, covert attention is manipulated by presenting a pre-cue, prior to the target –and
137 the aforementioned studies also did so (see **Table 1**). However, endogenous post-cues, pre-
138 sented after target offset, can also improve performance by affecting the information readout
139 (Kinchla et al., 1995; Nobre et al., 2004a; Ruff et al., 2007; Hulme et al., 2009) and modulate
140 fMRI activity in early visual areas (Nobre et al., 2004a; Hulme et al., 2009; Pestilli et al., 2011;
141 Sergent et al., 2011). Exogenous post-cues also affect performance in some tasks (Sergent et
142 al., 2013; Thibault et al., 2016), but not in others (Carrasco and Yeshurun, 1998; Gobell and
143 Carrasco, 2005; Anton-Erxleben et al., 2007; Fuller et al., 2009), and the only study evaluating
144 post-cues in exogenous attention showed no such modulation (Liu et al., 2005). Critically, no
145 single study has compared visual cortex activity with post-cues in endogenous and exogenous
146 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 SOA=100 or 800 ms	luminance change of peripheral placeholder 50% valid	X	RT	Group-averaged	Occipital: <i>Cuneus, MOG, SOG</i> + Frontal Temporo-Parietal	No	No
Peelen et al., 2004	central arrow 75% valid SOA=550 ms	brightening of peripheral placeholder 50% valid	square	RT	Group-averaged	Occipital: <i>Cuneus</i> + Frontal Temporo-Parietal	No	No
Natale et al., 2006	single peripheral rectangular frame 100% valid SOA=8, 8.15, 8.3, 8.45 or 8.6 s	five peripheral rectangular frames 20% valid	a black and white checkerboard	RT for 4 out of 8 participants	Group-averaged	Occipital: <i>Fusiform, TOS, LG, SC, LOG</i> + Frontal Temporo-Parietal	No	No
Discrimination tasks								
Kincade et al., 2005	brightening of half of central fixation diamond 75% valid SOA=2160 ms	color singleton in an array of colored squares 50% valid	T vs. L	RT (% correct)	Group-averaged	Occipital: <i>LO, MT, Cuneus, Fusiform, SOG</i> + Frontal Temporo-Parietal	No	No
Esterman et al., 2008	color change of a peripheral placeholder 75% valid SOA=300 ms	50% valid	face identity	RT (% correct)	ROI-based (FFA) + Group-averaged	Occipital: <i>FFA</i> + 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: <i>V1, V2, V3, V3A, hV4, LO1</i>	Yes	Yes
Studies NOT including Occipital areas								
Detection tasks								
Rosen et al., 1999	central arrow 80% valid SOA=400, 550 or 700 ms	peripheral dot 50% valid	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 placeholder 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 peripheral 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 peripheral placeholder 50% valid SOA=100–300 ms	central color of a check-erboard	Inverse efficiency = RT/%correct	Group-averaged	Frontal Temporo-Parietal	No	No

147

148 **Table 1. fMRI studies comparing endogenous and exogenous attention independently in human participants.** For each study, we report the
 149 cueing manipulation for each attention condition (SOA: Stimulus Onset Asynchrony is the duration of the cue + interval before onset of the target),
 150 the task performed by the participants, the dependent variable reported in the publication, whether the analysis was based on group-averaging or
 151 ROI-based on single-participants, the cortical areas reported in the publications and showing significant activation due to cue and/or target, whether
 152 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
 153 behavioral measures. IOG: Inferior Occipital Gyrus; LG: Lingual Gyrus; LO: Lateral Occipital area; LOG: Lateral Occipital Gyrus; MOG: Middle
 154 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 Doshier, 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.

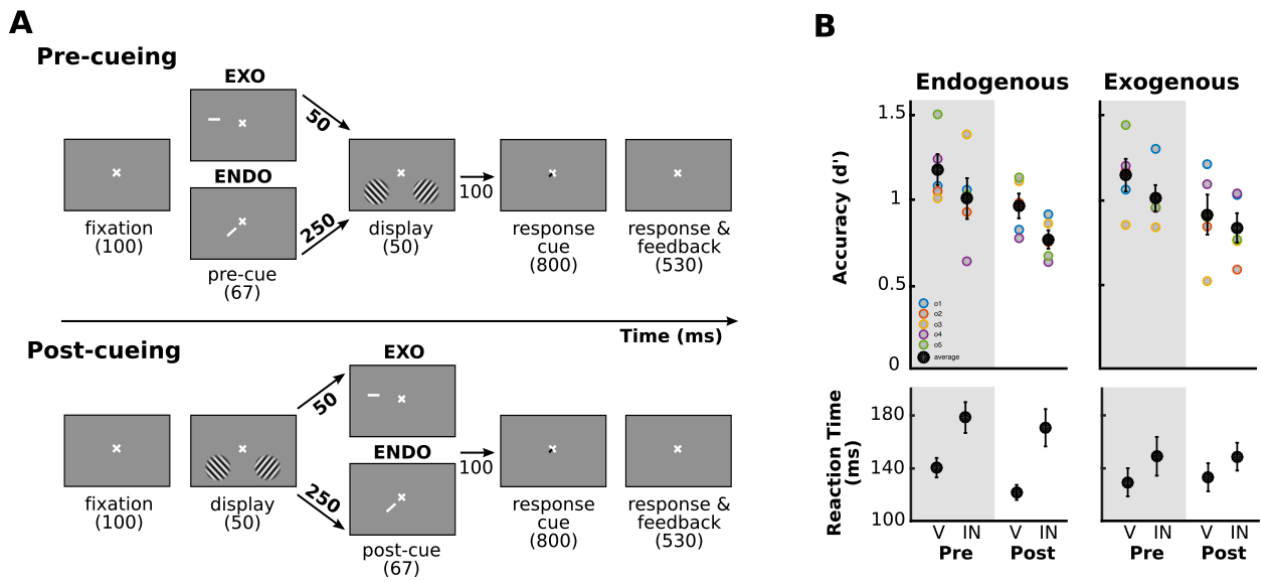
196

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 ($F<1$).



210

211 **Figure 1. Experimental protocol. A.** Participants performed a 2-AFC orientation-discrimination
 212 task. (The display is not at scale for visibility purposes). Pre-cues and post-cues were presented
 213 before and after the stimuli, respectively. Exogenous cues appeared in the periphery, above one
 214 of the two stimulus locations. Endogenous cues appeared at the center of the screen and indi-
 215 cated one of the two stimulus locations. The ISI between the cue and the gratings was shorter for
 216 the exogenous (50 ms) than the endogenous (250 ms) conditions. A response cue indicated the
 217 target location and instructed participants to indicate whether the target grating was tilted clock-
 218 wise or counterclockwise of vertical by pressing one of two keys. To provide feedback, the fixa-
 219 tion-cross turned green or red for a correct or an incorrect answer, respectively. **B.** Behavioral
 220 performance averaged across participants (black dots) and for each of them (colored dots; $n=5$)
 221 for endogenous (left) and exogenous (right) attention. (Top) Performance accuracy (d' ; top) and
 222 median reaction time (bottom) as a function of cueing condition. V, valid cue (same location of
 223 pre-cue/post-cue as response cue). IN, invalid cue (different location of pre-cue/post-cue than
 224 response cue). Pre, pre-cue presented before the stimuli. Post, post-cue presented after the
 225 stimuli. Valid cues induced more accurate and faster responses (there was no speed-accuracy
 226 trade-off). Error bars, ± 1 SEM across participants.

227

228 In each condition, we also calculated reaction time for each participant separately (**Figure**
 229 **1B**, bottom row). A three-way repeated measures ANOVA revealed faster reaction times for valid
 230 than invalid cues ($F(1,4)=62.3$, $p=0.001$). There was no significant difference between exogenous
 231 and endogenous cues ($F(1,4)=2.7$, $p=0.17$), or between pre- and post-cues ($F(1,4)=1.7$, $p=0.27$).
 232 Two significant interactions indicated that the differences between valid and invalid cues
 233 ($F(1,4)=16.2$, $p=0.02$) and between pre- and post-cues ($F(1,4)=8.1$, $p=0.047$) were more pro-
 234 nounced for endogenous attention than for exogenous attention.

235 These behavioral results, which are consistent with previous findings (Lu and Doshier,
 236 1998; Carrasco et al., 2000; Doshier and Lu, 2000; Ling and Carrasco, 2006b; Giordano et al.,
 237 2009; Pestilli et al., 2009; Herrmann et al., 2010), show that attention improved orientation

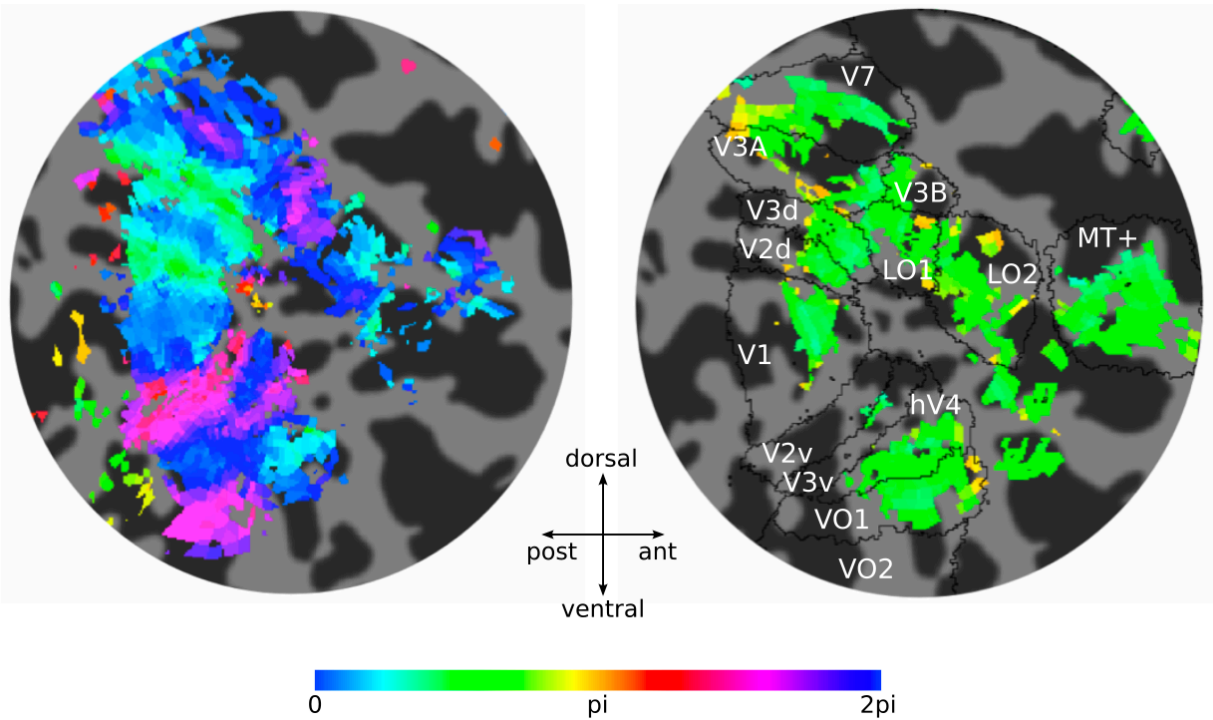
238 discrimination (d' and reaction time), with no evidence of a speed-accuracy trade-off, and similarly
239 for both types of attention and for both pre- and post-cues. Thus, the behavioral effects confirm
240 the successful manipulation of endogenous and exogenous attention, for both pre- and post-
241 cues, consistently across individuals.

242

243 **Attentional modulation of perceptual and post-perceptual information processing in vis-** 244 **ual cortex**

245 Visual areas were mapped in each participant following retinotopic mapping procedures
246 (**Figure 2**, left panel) and a targeted stimulus localizer (**Figure 2**, right panel), and regions of
247 interest (ROIs) were selected based on previous literature: V1, V2, V3 (for V2 and V3, ventral
248 and dorsal ROIs were averaged), V3A, hV4 and LO1 (e.g., Engel et al., 1994; Sereno et al., 1995;
249 Engel et al., 1997; Larsson and Heeger, 2006; Wandell et al., 2007).

250 Activity was higher for contralateral than ipsilateral brain areas. For each ROI, we meas-
251 ured the fMRI response amplitudes for each type of attention – exogenous and endogenous –
252 and each cueing condition – pre- and post-cueing, for the contralateral and ipsilateral side to the
253 cued (attended) location. We analyzed the fMRI responses evoked by each type of attention in
254 the contralateral and ipsilateral brain regions relative to the cue location (**Supplemental Figure**
255 **1**). ANOVAs indicated that there was higher contralateral than ipsilateral activity across brain
256 areas (endogenous: $F(1,4)=59.9$, $p=0.0015$; exogenous: $F(1,4)=218.8$, $p=0.0001$). For both types
257 of attention, this difference was more pronounced for valid than invalid cues (endogenous:
258 $F(1,4)=8.6$, $p=0.04$; exogenous: $F(1,4)=21.1$, $p=0.01$). In the following analyses, we then concen-
259 trate on fMRI activity in the contralateral ROIs to the attended location.

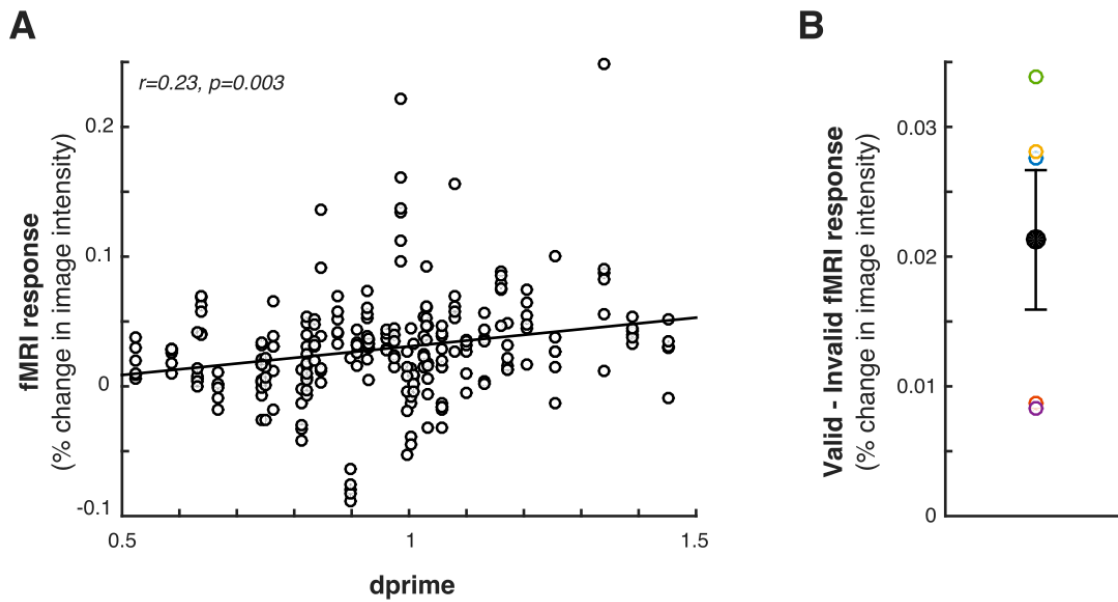


260

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

267

268 fMRI responses correlated with behavioral variability. We evaluated the degree to which
269 inter-individual variability in behavioral performance co-varied with variability in fMRI responses.
270 We computed the correlation (**Figure 3A**), across participants, ROIs, types of attention and cue-
271 ing conditions, between the fMRI responses (percent change in image intensity) and behavioral
272 performance accuracy (d'). We found a positive correlation between fMRI activity and d' (Pearson
273 correlation $r = 0.23$, $p = 0.003$), which was present for both attention types (endogenous: Pearson
274 correlation $r = 0.3$, $p = 0.003$; exogenous: $r = 0.2$, $p = 0.02$). We further showed that fMRI activity
275 was overall higher for valid than invalid trials ($t(4) = 4.0$, $p = 0.0163$, Cohen's $d = 1.78$). This was
276 the case for each participant (**Figure 3B**). Together, these results are consistent with previous
277 findings showing that fMRI response correlates with behavioral variability (Ress et al., 2000;
278 Giesbrecht et al., 2006; Liu et al., 2007a), and that attentional orienting increases fMRI signal in
279 early visual cortex (for review Beck and Kastner, 2014).

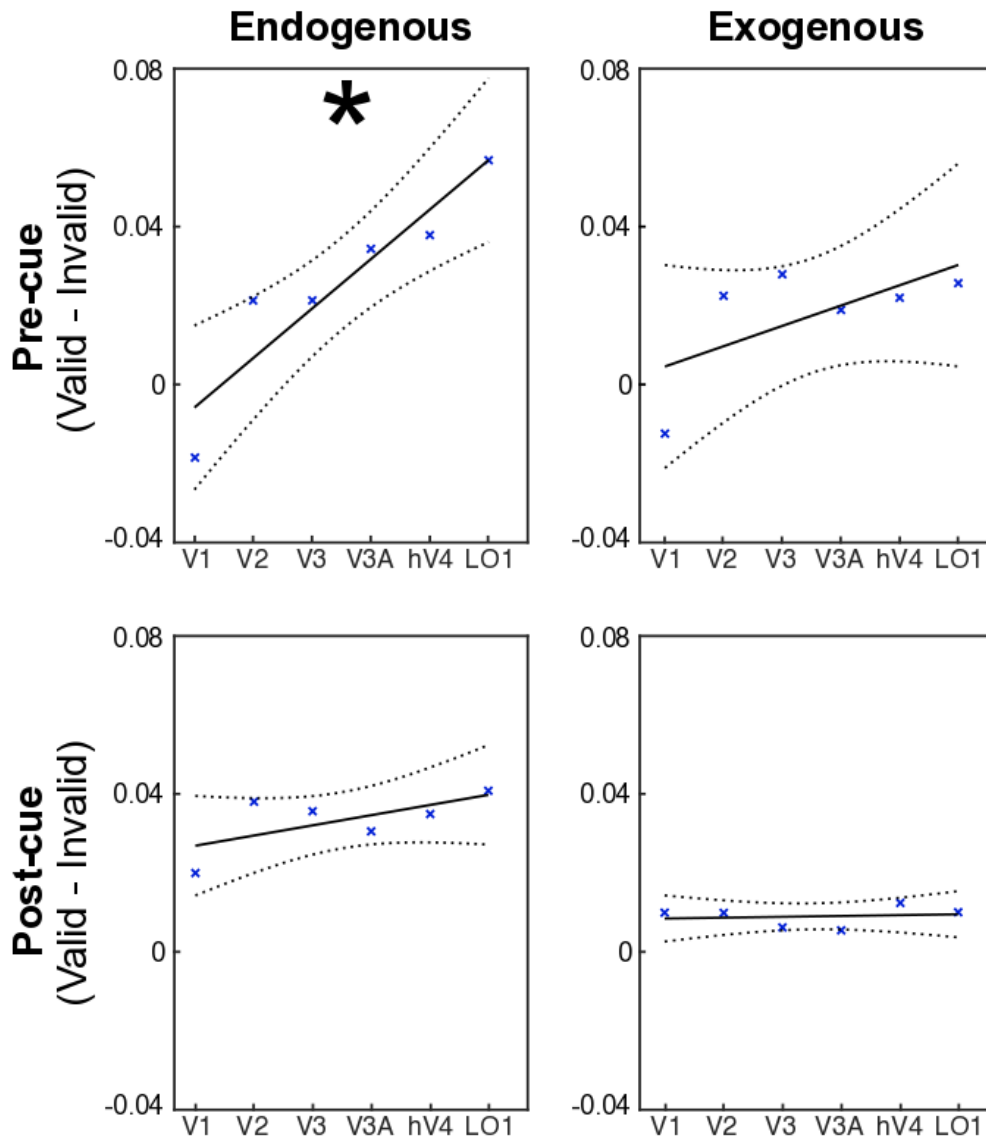


280

281 **Figure 3. Inter-individual fMRI response. A.** Positive correlation between fMRI response and
282 behavioral performance (Pearson correlation $r = 0.23$, $p = 0.003$). Each dot indicates fMRI re-
283 sponse amplitude measured from one ROI and one participant, separately for each attentional
284 condition (pre and post-cue, valid and invalid). **B.** fMRI response difference between valid and
285 invalid trials combined across all conditions and ROIs for each participant (colored dots), and
286 across participants (black dot; average significantly positive: $t(4) = 4.0$, $p = 0.0163$, Cohen's $d =$
287 1.78). Error bar, ± 1 SEM across participants.

288

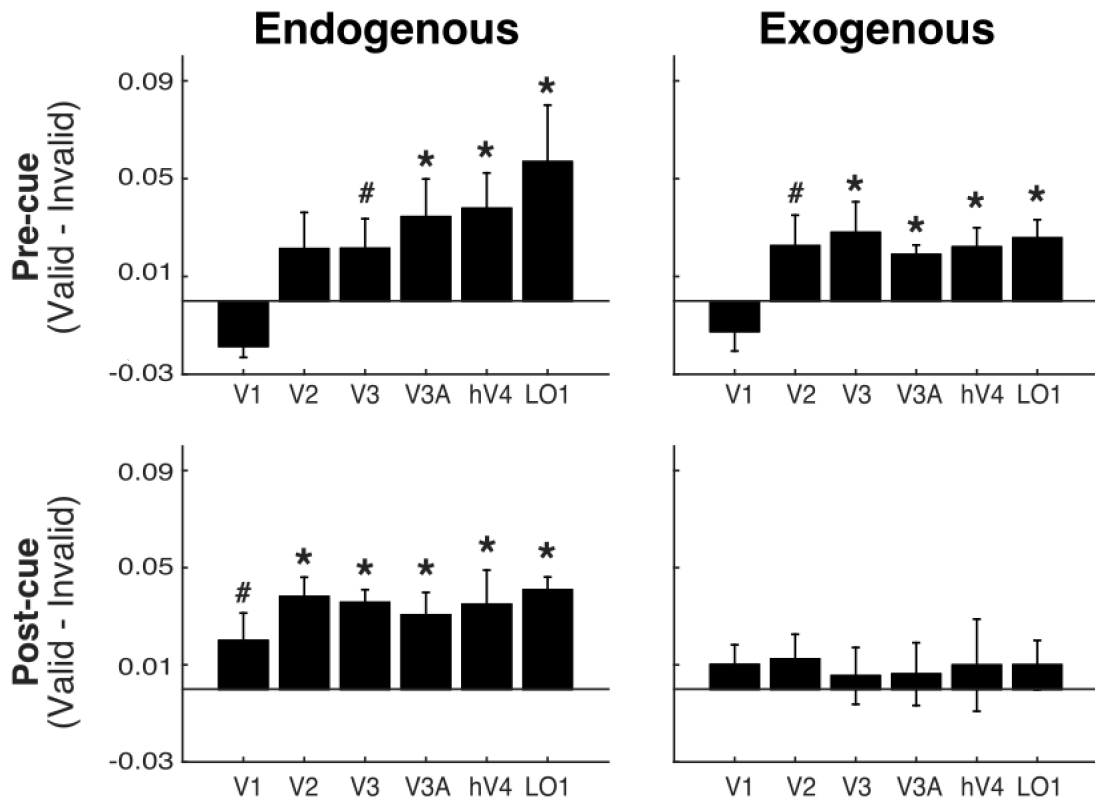
289 We then tested our two novel predictions: (1) attentional modulation of fMRI stimulus-
290 evoked activity increases along the visual hierarchy for endogenous pre-cueing, but is constant
291 for exogenous pre-cueing; and (2) attentional modulation of fMRI stimulus-evoked activity for
292 endogenous post-cueing is constant along the visual hierarchy, whereas there is no attentional
293 modulation for exogenous post-cueing. We measured the differences in activity between valid
294 and invalid trials for each type of attention and for pre- and post-cues, across the hierarchy of
295 visual cortical areas (**Figure 4**). Regression analyses showed a significant increase along the
296 hierarchy of the visual areas of the activity difference evoked by valid and invalid trials for the
297 endogenous pre-cueing condition ($F = 25.8$, $p = 0.007$, $R^2 = 0.87$), but not for the exogenous pre-
298 cueing condition ($F = 2.8$, $p = 0.168$, $R^2 = 0.41$), endogenous post-cueing ($F = 3.0$, $p = 0.161$, R^2
299 $= 0.42$) or exogenous post-cueing conditions ($F = 0.1$, $p = 0.774$, $R^2 = 0.02$). The differential
300 effects of these regression analyses are consistent with post-hoc t-tests performed for each con-
301 dition and ROI (**Figure 5**).



302

303 **Figure 4. Specificity of pre and post-cueing for endogenous and exogenous attention.** The
304 difference in fMRI response between valid and invalid is plotted separately for pre- and post-cue
305 conditions for each ROI. *, Statistically significant regression analysis ($p < 0.05$).
306

307 For both endogenous attention ($p < 0.05$ for V3a, V4 and LO1; trend ($p = 0.077$) for V3; t-
308 tests) and exogenous attention ($p < 0.05$ for V3, V3A, hV4 and LO1; trend ($p = 0.074$) for V2; t-
309 tests) pre-cues elicited greater fMRI activity for valid than invalid cues (**Figure 5**, top-left and top-
310 right panels). Furthermore, for endogenous attention ($p < 0.05$ for V2, V3, V3A, hV4 and LO1;
311 trend ($p = 0.077$) for V1; t-tests; **Figure 5**, bottom-left panel), but not for exogenous attention (all
312 $p > 0.1$; t-tests; **Figure 5**, bottom-right panel), post-cues elicited greater fMRI activity for valid
313 than invalid cues in occipital areas (detailed statistics are presented in Supplementary Table 1).
314 Taken together, these results confirm both of our predictions.



315

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

321

322

323

324

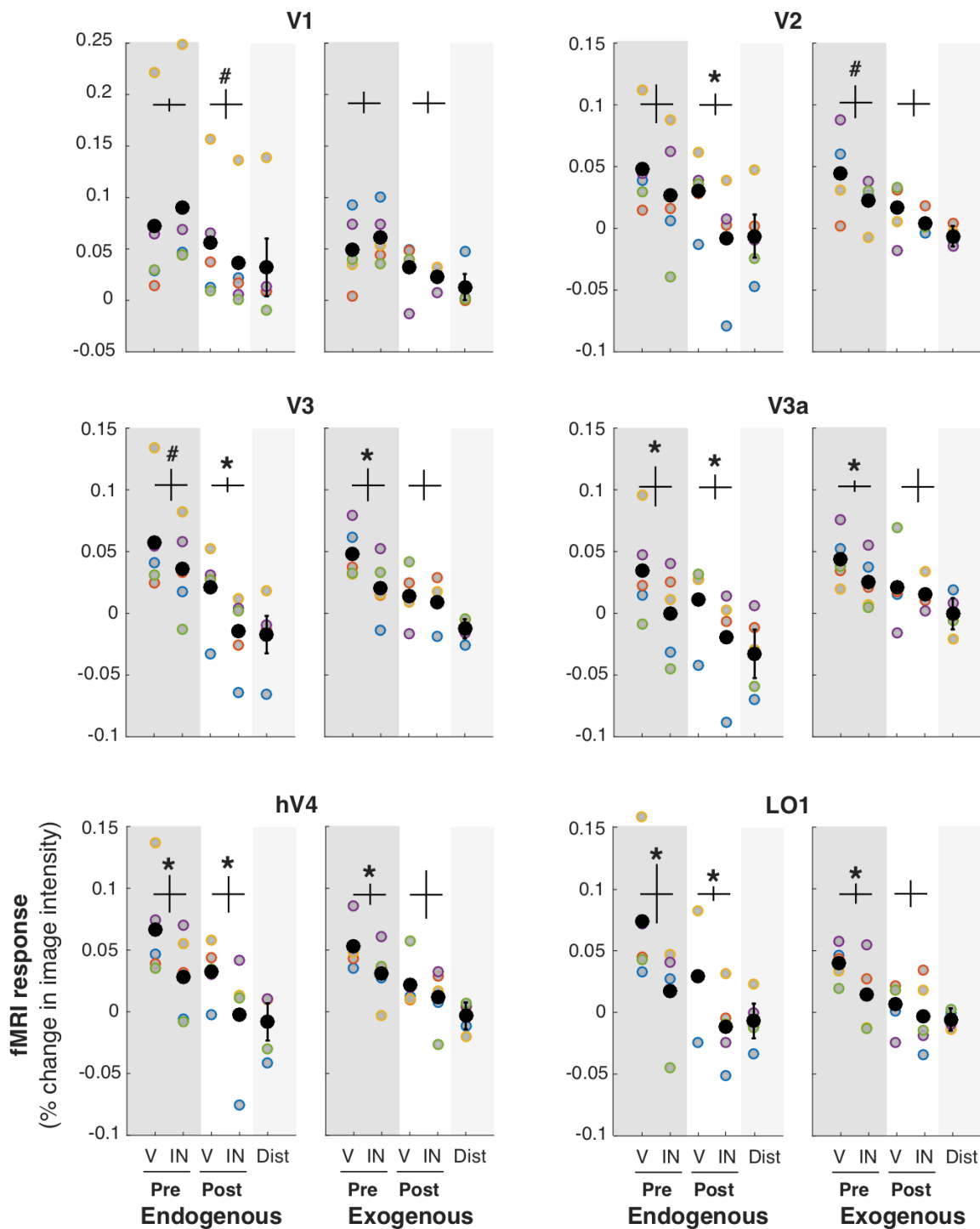
325

326

327

328

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 \times 2 pre/post-cue \times 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 ($F = 4.1$, $p = 0.0103$).



329
330
331
332
333
334
335
336
337
338
339
340

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.

341 **DISCUSSION**

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

348 Previous studies comparing endogenous and exogenous attention conditions state vari-
349 ous attentional effects in early visual areas (see **Table 1**). Some report differential effects be-
350 tween these attention conditions in the right LO and MT (Kincade et al., 2005), others in the
351 cuneus (Peelen et al., 2004; Mayer et al., 2004; Kincade et al., 2005), the occipital gyrus (SOG,
352 MOG, LOG; Mayer et al., 2004; Kincade et al., 2005; Natale et al., 2006), the fusiform area (Kin-
353 cade et al., 2005; Natale et al., 2006; Esterman et al., 2008), and the TOS, LG and SC (Natale
354 et al., 2006). This lack of clear picture regarding the differential impact of endogenous and exog-
355 enous spatial attention is likely due to the methodological differences and limitations we dis-
356 cussed in the Introduction (see also **Table 1**). In any case, it is often assumed that the effects of
357 endogenous and exogenous attention are the same in visual occipital areas (Corbetta and Shul-
358 man, 2002; Peelen et al., 2004; Corbetta et al., 2008; Chica et al., 2013; Beck and Kastner,
359 2014).

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

369 There was an overall positive correlation between performance in the orientation discrim-
370 ination task and the degree of attentional modulation in fMRI activity. This result was expected,
371 indicating that as discriminability increases so does the attentional modulation in fMRI activity.
372 But only very few studies on the effect of spatial attention in early visual areas have reported
373 such a correlation (Ress et al., 2000; Giesbrecht et al., 2006; Liu et al., 2007a). The behavioral
374 effects obtained in the scanner are consistent with psychophysical studies. The enhanced per-
375 formance brought about by the valid, but uninformative peripheral pre-cue is consistent with an
376 automatic, bottom-up involuntary capture of exogenous attention (e.g. Doshier and Lu, 2000; Car-
377 rasco et al., 2000; Carrasco et al., 2004; Pestilli and Carrasco, 2005; Giordano et al., 2009; Herr-
378 mann et al., 2010; Fernández et al., 2019). The enhanced performance brought about by the
379 valid, informative central precue is consistent with a top-down, voluntary deployment of endoge-
380 nous attention (e.g. Doshier and Lu, 2000; Ling and Carrasco, 2006c; Giordano et al., 2009; Liu
381 et al., 2009; Herrmann et al., 2010; Poletti et al., 2017; Jigo and Carrasco, 2018).

382 In the endogenous attention condition, there was an increase in attentional modulation of
383 stimulus-evoked activity along the hierarchy of visual areas. There is no consensus regarding the
384 visual hierarchy beyond area V3 (e.g. Harvey and Dumoulin, 2011; Harvey and Dumoulin, 2016;
385 Michalareas et al., 2016; Yildirim et al., 2018; Fritsche et al., 2020), especially regarding V3A.
386 However, most authors agree that hV4 precedes LO1 (Harvey and Dumoulin, 2011; Harvey and
387 Dumoulin, 2016; Michalareas et al., 2016; Yildirim et al., 2018). In any case, our data are con-
388 sistent with either a strict hierarchy or with V3A and hV4 being at the same level. Such a pattern
389 is consistent with previous studies suggesting that endogenous attention is a top-down modula-
390 tion from frontal and parietal areas feeding back to visual cortex, with diminishing effects in earlier
391 visual areas (Kastner et al., 1999; Maunsell and Cook, 2002; Kastner and Pinsk, 2004; Chica et
392 al., 2013). Inconsistent with previous studies (e.g. Boynton et al., 1999; Brefczynski and DeYoe,
393 1999; Somers et al., 1999; Herrmann et al., 2010; Pestilli et al., 2011), there was no evidence for
394 attentional modulation in V1. It might be that attentional modulation of V1 activity is more variable
395 than other visual cortical areas, making it harder to detect (see also Kastner et al., 1999; Liu et
396 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; Mulckhuysen 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 is 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

453 exogenous attention. Together, these two studies provide a comprehensive investigation of en-
454 dogenous and exogenous attention, and pave the way for rigorous psychophysics informed, neu-
455 roimaging studies of covert, spatial attention. Here, we concentrated the analysis on visual corti-
456 cal areas in the occipital lobe because the slice prescription covered only a limited portion of the
457 brain. The present findings further our knowledge of the neurophysiological bases of covert at-
458 tention and have implications for models of visual attention, which should consider not only the
459 similarities, but also the differences in the orienting and reorienting of endogenous and exoge-
460 nous attention in occipital areas reported here.

461 In conclusion, the present results show some similarities and reveal important differences
462 in the specific neural correlates of endogenous and exogenous attention on early vision: An in-
463 creasing modulation of fMRI activity for pre-cueing endogenous attention, but constant modula-
464 tion for exogenous attention, along the hierarchy of visual occipital areas, as well as a reliable
465 and constant modulation of fMRI activity for post-cueing endogenous attention in occipital areas
466 but not for exogenous attention. These results suggest that endogenous attention facilitates both
467 the encoding and the readout of visual information whereas exogenous attention only facilitates
468 the encoding of information.

469

470 **MATERIALS and METHODS**

471 The behavioral methods employed in this study and the behavioral results are the same
472 as those we reported in a recent study, in which we compared activity in TPJ during orienting and
473 reorienting of endogenous and exogenous attention (Dugué et al., 2017a). To maximize the ef-
474 fects of these two types of attention, i.e. the benefits at the attended location and concurrent
475 costs at the unattended location, we used optimal spatial and temporal parameters (reviews by
476 Carrasco, 2011; Carrasco and Barbot, 2015). To enable direct comparison between endogenous
477 and exogenous attention, the same participants performed the same orientation discrimination
478 task under both types of attention. The fMRI methods employed in this study are the same as
479 those used in that study (Dugué et al., 2017a), but here, instead of analyzing TPJ activity, we
480 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 Involving
484 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

509 upcoming grating stimulus, vertically aligned with the stimulus and above the horizontal merid-
510 ian (1° away from the edge of the grating stimulus; and the edge of the cue 4.44° horizontal
511 eccentricity from the edge of the fixation cross).

512 **Behavioral procedure**

513 An exogenous attention condition trial lasted 1700 ms, whereas an endogenous attention
514 condition trial lasted 1900 ms, the only difference being the stimulus-onset asynchronies (SOA)
515 between the cue and the display; the timing of all the visual stimuli was the same in both attention
516 conditions (**Figure 1**; the display is not at scale for illustration purposes). In the pre-cue condition
517 (40% of the trials), a cue preceded the two gratings. In 40% the post-cue condition, the cue
518 followed the presentation of the gratings. In 'cue-only' trials (10% of the trials), the gratings were
519 not presented. In 'blank' trials (10% of the trials), neither a cue nor the gratings were presented.
520 These trials were then included in the GLM analysis to model the contribution of the visual signal
521 produced by the cue (see MRI procedure). For both pre-cue and post-cue trials, participants were
522 asked to press one of two keys to report the orientation of a target grating, i.e., clockwise or
523 counter-clockwise compared to vertical. Participants pressed a third key in the case of cue-only
524 and blank trials.

525 In both exogenous and endogenous condition, cues were presented for 67 ms, indicating
526 either the bottom left or right quadrant of the screen. The inter-stimulus interval (ISI) between the
527 cue and the grating stimuli was 50 ms for exogenous and 250 ms for endogenous conditions,
528 resulting in SOA of 117 ms and 317 ms. We used the same timings for pre- and post-cue condi-
529 tions (e.g. Kinchla et al., 1995; Carrasco and Yeshurun, 1998; Liu et al., 2005; Pestilli et al.,
530 2011). These delays are optimal to manipulate exogenous and endogenous attention, while
531 keeping the trial duration as similar as possible, and have been shown to maximize the behavioral
532 consequences of each attention condition (Nakayama and Mackeben, 1989; Mackeben and Na-
533 kayama, 1993; Liu et al., 2007b; Müller, 2014).

534 The behavioral effects of endogenous attention are sustained (e.g. Ling and Carrasco,
535 2006c) and thus, as shown in ERP studies (e.g. Seiss et al., 2009), are still present in later brain

536 activity. Additionally, during 300 ms following cue onset, the brain responses elicited by exoge-
537 nous and endogenous cues differ (for review Carrasco 2011). The two grating stimuli were then
538 displayed for 50 ms. For the postcue trials we kept the timings of cue and stimuli constant but
539 inverted the order of their presentation (e.g. Kinchla et al., 1995; Carrasco and Yeshurun, 1998;
540 Liu et al., 2005; Pestilli et al., 2011). A response cue, presented for 800 ms at the end of the trial
541 after both the cue and the stimuli had disappeared, indicated which one of the two gratings was
542 the target (50% of the trials on the right and the remaining 50% and on the left). The maximum
543 delay between the offset of the grating stimuli and the onset of the response cue was shorter
544 (~400 ms max in the endogenous condition) than typically associated with a demand for working
545 memory (>600 ms; Phillips, 1974). Immediately following each trial, a change of color of the fix-
546 ation cross provided visual feedback to the participants, i.e. green for correct or red for incorrect
547 responses. The fixation cross did not change color if participants had missed the response win-
548 dow, i.e. if they had not pressed any key after 530 ms.

549 In the exogenous attention condition, a peripheral cue was presented, which was not in-
550 formative regarding the target location or orientation. When the cue location matched the target
551 location, it was considered a valid trial (50% of the trials), otherwise it was considered an invalid
552 trial (the remaining 50% of the trials). In the endogenous attention condition, a central cue pointed
553 to either the left or right quadrant. The cue was informative of the target location but not its ori-
554 entation (75% valid trials and 25% invalid trials). Participants were informed of this validity. It is
555 important to notice that cue validity does not affect cueing effectiveness for exogenous attention,
556 although it does so do endogenous attention (e.g. Sperling and Melchner, 1978; Kinchla, 1980;
557 Giordano et al., 2009).

558 Endogenous and exogenous attention conditions were performed in separate sessions to
559 ensure optimal manipulation of each attention system. Participants first performed two practice
560 sessions outside the scanner before the first session of each attentional scanning condition. To
561 equate task difficulty for both attention conditions, using a staircase procedure, the tilt of the
562 target grating was adjusted for each participant to achieve ~80% correct performance in the valid
563 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;

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

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

599 *Retinotopic mapping.* We followed well-established conventional traveling-wave, phase-
600 encoded methods. Using clockwise and counter-clockwise rotating checkerboard wedges, we
601 measured phase maps of polar angle. Using contracting and expanding checkerboard rings, we
602 measured eccentricity maps (Engel et al., 1994; Sereno et al., 1995; Engel et al., 1997; Larsson
603 and Heeger, 2006; Wandell et al., 2007). **Figure 2** (left panel) shows the visual areas that were
604 drawn by hand on flattened surface of the brain, following published conventions (Engel et al.,
605 1997; Larsson and Heeger, 2006; Wandell et al., 2007; Liu et al., 2007a).

606 *Stimulus localizer.* In each scanning session of the main experiment, participants com-
607 pleted one stimulus localizer run (6 runs overall, 4 min each). A run consisted of 16 cycles (17.5 s)
608 of a block alternation protocol between stimulus on (8.75 s) and stimulus off (8.75 s). Participants
609 only had to fixate the central cross throughout each run. The stimuli were at the same location,
610 and of the same size and spatial frequency as those in the main experiment, except at full con-
611 trast and their phase and orientation changed randomly every 200 ms to avoid adaptation. To
612 define the cortical representation of the gratings, we then averaged the data across the 6 runs
613 and followed the same methods as for the retinotopic mapping. Voxels that responded positively
614 during the blocks when the grating stimuli were presented were used to restrict each retinotopic
615 ROI. The fMRI time series from each voxel were fit to a sinusoid. To be conservative, only voxels
616 whose best-fit sinusoid had a phase value between 0 and pi, and a coherence between the best-
617 fit sinusoid and the time series greater than 0.2 were included in the ROI (**Figure 2**, right panel).
618 Analysis performed without restricting the ROI to this coherence level yielded similar results.

619 *Event-related analysis.* fMRI time series were averaged across voxels in each ROI (sep-
620 arately for each hemisphere) and then concatenated across runs. The data were denoised using
621 GLMDenoise (Kay et al., 2013a), and fMRI response amplitudes were computed using linear
622 regression, with twelve regressors: 8 combinations of right and left valid and invalid pre- and
623 post-cue, right and left cue-only, blank (no cue nor stimulus) and eye-movements (blink or broken
624 fixation). For each ROI in each hemisphere, the resulting fMRI response amplitudes (for correct
625 trials only) were then averaged across participants.

626

627 **Acknowledgments:** This work was supported by: NIH RO1-EY019693 to MC and DJH; NIH
628 RO1-EY027401 to MC; the FYSSSEN Foundation and the Philippe Foundation to LD; and the
629 Center for Brain Imaging of New York University. We want to thank members of the Carrasco lab
630 for constructive comments on the manuscript. The authors declare no conflicts of interest.

631 **REFERENCES**

- 632 Anton-Erxleben K, Carrasco M (2013) Attentional enhancement of spatial resolution: linking be-
633 havioural and neurophysiological evidence. *Nat Rev Neurosci* 14:188–200.
- 634 Anton-Erxleben K, Henrich C, Treue S (2007) Attention changes perceived size of moving visual
635 patterns. *Journal of Vision* 7:1–9.
- 636 Barbot A, Carrasco M (2017) Attention Modifies Spatial Resolution According to Task Demands.
637 *Psychological Science* 28:285–296
- 638 Barbot A, Landy MS, Carrasco M (2012) Differential effects of exogenous and endogenous at-
639 tention on second-order texture contrast sensitivity. *Journal of Vision* 12:1–15.
- 640 Beauchamp MS, Petit L, Ellmore TM, Ingelholm J, Haxby JV (2001) A parametric fMRI study of
641 overt and covert shifts of visuospatial attention. *Neuroimage* 14:310–321.
- 642 Beck DM, Kastner S (2009) Top-down and bottom-up mechanisms in biasing competition in the
643 human brain. *Vision Res* 49:1154–1165.
- 644 Beck DM, Kastner S (2014) Neural systems for spatial attention in the human brain: Evidence
645 from neuroimaging in the framework of biased competition. *The Oxford Handbook of Atten-*
646 *tion*:253–288.
- 647 Bloem IM, Ling S (2019) Normalization governs attentional modulation within human visual cor-
648 tex. *Nature Communications* 10:5660–10.
- 649 Bowling JT, Friston KJ, Hopfinger JB (2019) Top-down versus bottom-up attention differentially
650 modulate frontal–parietal connectivity. *Hum Brain Mapp* 9:1116.
- 651 Boynton GM, Demb JB, Glover GH, Heeger DJ (1999) Neuronal basis of contrast discrimination.
652 *Vision Res* 39:257–269.
- 653 Brefczynski JA, DeYoe EA (1999) A physiological correlate of the “spotlight” of visual attention.
654 *Nat Neurosci* 2:370–374.
- 655 Brouwer GJ, Arnedo V, Offen S, Heeger DJ, Grant AC (2015) Normalization in human soma-
656 tosensory cortex. *J Neurophysiol* 114:2588–2599.
- 657 Buracas GT, Boynton GM (2007) The effect of spatial attention on contrast response functions
658 in human visual cortex. *Journal of Neuroscience* 27:93–97.
- 659 Buschman TJ, Miller EK (2009) Serial, Covert Shifts of Attention during Visual Search Are Re-
660 flected by the Frontal Eye Fields and Correlated with Population Oscillations. *Neuron*
661 63:386–396.
- 662 Busse L, Katzner S, Treue S (2008) Temporal dynamics of neuronal modulation during exoge-
663 nous and endogenous shifts of visual attention in macaque area MT. *Proc Natl Acad Sci USA*
664 105:16380–16385.
- 665 Carrasco M (2011) Visual attention: the past 25 years. *Vision Res* 51:1484–1525.
- 666 Carrasco M, Barbot A (2015) How attention affects spatial resolution. *Cold Spring Harbor Sym-*
667 *posia on Quantitative Biology* 79:149–160.
- 668 Carrasco M, Evert DL, Chang I, Katz SM (1995) The eccentricity effect: target eccentricity affects
669 performance on conjunction searches. *Perception & Psychophysics* 57:1241–1261.

- 670 Carrasco M, Giordano AM, McElree B (2006) Attention speeds processing across eccentricity:
671 Feature and conjunction searches. *Vision Res* 46:2028–2040.
- 672 Carrasco M, Marie Giordano A, McElree B (2004) Temporal performance fields: visual and at-
673 tentional factors. *Vision Res* 44:1351–1365.
- 674 Carrasco M, McElree B (2001) Covert attention accelerates the rate of visual information pro-
675 cessing. *PNAS* 98:5363–5367.
- 676 Carrasco M, Penpeci-Talgar C, Eckstein M (2000) Spatial covert attention increases contrast
677 sensitivity across the CSF: support for signal enhancement. *Vision Res* 40:1203–1215.
- 678 Carrasco M, Yeshurun Y (1998) The contribution of covert attention to the set-size and eccen-
679 tricity effects in visual search. *Journal of Experimental Psychology: Human Perception and*
680 *Performance* 24:673–692.
- 681 Carrasco M, Yeshurun Y (2009) Covert attention effects on spatial resolution. *Prog Brain Res*
682 176:65–86.
- 683 Chica AB, Bartolomeo P, Lupiáñez J (2013) Two cognitive and neural systems for endogenous
684 and exogenous spatial attention. *Behavioural Brain Research* 237:107–123.
- 685 Chica AB, Lupiáñez J (2009) Effects of endogenous and exogenous attention on visual pro-
686 cessing: an Inhibition of Return study. *Brain Res* 1278:75–85.
- 687 Corbetta M, Patel G, Shulman GL (2008) The reorienting system of the human brain: from envi-
688 ronment to theory of mind. *Submitted* 58:306–324.
- 689 Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the
690 brain. *Nat Rev Neurosci* 3:201–215.
- 691 Correa Á, Triviño M, Pérez-Dueñas C, Acosta A, Lupiáñez J (2010) Temporal preparation, re-
692 sponse inhibition and impulsivity. *Brain and Cognition* 73:222–228.
- 693 Culham JC, Cavanagh P, Kanwisher NG (2001) Attention Response Functions: Characterizing
694 Brain Areas Using fMRI Activation during Parametric Variations of Attentional Load. *Neuron*
695 32:737–745.
- 696 Doricchi F, Macci E, Silvetti M, Macaluso E (2010) Neural correlates of the spatial and expectancy
697 components of endogenous and stimulus-driven orienting of attention in the Posner task.
698 *Cereb Cortex* 20:1574–1585.
- 699 Doshier BA, Lu ZL (2000) Mechanisms of perceptual attention in precuing of location. *Vision Res*
700 40:1269–1292.
- 701 Dugué L, Merriam EP, Heeger DJ, Carrasco M (2017a) Specific Visual Subregions of TPJ Medi-
702 ate Reorienting of Spatial Attention. *Cereb Cortex*:1–16.
- 703 Dugué L, Roberts M, Carrasco M (2016) Attention Reorients Periodically. *Current Biology*
704 26:1595–1601.
- 705 Dugué L, Xue AM, Carrasco M (2017b) Distinct perceptual rhythms for feature and conjunction
706 searches. *Journal of Vision* 17:22–22.
- 707 Engel SA, Glover GH, Wandell BA (1997) Retinotopic organization in human visual cortex and
708 the spatial precision of functional MRI. *Cereb Cortex* 7:181–192.

- 709 Engel SA, Rumelhart DE, Wandell BA, Lee AT, Glover GH, ED C, Shadlen MN (1994) fMRI of
710 human visual cortex. *Nature* 369:525.
- 711 Esterman M, Prinzmetal W, DeGutis J, Landau AN, Hazeltine E, Verstynen T, Robertson L (2008)
712 Voluntary and involuntary attention affect face discrimination differently. *Neuropsychologia*
713 46:1032–1040.
- 714 Fernández A, Li H-H, Carrasco M (2019) How exogenous spatial attention affects visual repre-
715 sentation. *Journal of Vision* 19:4.
- 716 Freeman J, Heeger DJ, Merriam EP (2013) Coarse-scale biases for spirals and orientation in
717 human visual cortex. *Journal of Neuroscience* 33:19695–19703.
- 718 Fuller S, Park Y, Carrasco M (2009) Cue contrast modulates the effects of exogenous attention
719 on appearance. *Vision Res* 49:1825–1837.
- 720 Gardner JL, Merriam EP, Movshon JA, Heeger DJ (2008) Maps of Visual Space in Human Oc-
721 cipital Cortex Are Retinotopic, Not Spatiotopic. *J Neurosci* 28:3988–3999.
- 722 Gardner JL, Merriam EP, Schluppeck D, Besle J, Heeger DJ (2018a) mrTools: Analysis and
723 visualization package for functional magnetic resonance imaging data. Available at:
724 <http://doi.org/10.5281/zenodo.1299483>.
- 725 Gardner JL, Merriam EP, Schluppeck D, Larsson J (2018b) MGL: Visual psychophysics stimuli
726 and experimental design package. Available at: <http://doi.org/10.5281/zenodo.1299497>.
- 727 Geng JJ, Vossel S (2013) Re-evaluating the role of TPJ in attentional control: contextual updat-
728 ing? *Neurosci Biobehav Rev* 37:2608–2620.
- 729 Giesbrecht B, Weissman DH, Woldorff MG, Mangun GR (2006) Pre-target activity in visual cortex
730 predicts behavioral performance on spatial and feature attention tasks. *Brain Res* 1080:63–
731 72.
- 732 Giordano AM, McElree B, Carrasco M (2009) On the automaticity and flexibility of covert atten-
733 tion: a speed-accuracy trade-off analysis. *Journal of Vision* 9:30.1–.10.
- 734 Gobell J, Carrasco M (2005) Attention alters the appearance of spatial frequency and gap size.
735 *Psychological Science* 16:644–651.
- 736 Hahn B, Ross TJ, Stein EA (2006) Neuroanatomical dissociation between bottom-up and top-
737 down processes of visuospatial selective attention. *Neuroimage* 32:842–853.
- 738 Heinen K, Ruff CC, Bjoertomt O, Schenkluhn B, Bestmann S, Blankenburg F, Driver J, Chambers
739 CD (2011) Concurrent TMS-fMRI reveals dynamic interhemispheric influences of the right
740 parietal cortex during exogenously cued visuospatial attention. *European Journal of Neuro-
741 science* 33:991–1000.
- 742 Herath P, Klingberg T, Young J, Amunts K, Roland PE (2001) Neural Correlates of Dual Task
743 Interference Can be Dissociated from Those of Divided Attention: an fMRI Study | *Cerebral
744 Cortex* | Oxford Academic. *Cereb Cortex* 11:796–805.
- 745 Herrmann K, Montaser-Kouhsari L, Carrasco M, Heeger DJ (2010) When size matters: attention
746 affects performance by contrast or response gain. *Nat Neurosci* 13:1554–1559.
- 747 Hulme OJ, Friston KF, Zeki S (2009) Neural correlates of stimulus reportability. *Cognitive Neu-
748 roscience, Journal of* 21:1602–1610.

- 749 Jigo M, Carrasco M (2018) Attention alters spatial resolution by modulating second-order pro-
750 cessing. *Journal of Vision* 18:2.
- 751 Kastner S, Pinsk MA (2004) Visual attention as a multilevel selection process. *Cognitive, Affec-
752 tive, & Behavioral Neuroscience* 4:483–500.
- 753 Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG (1999) Increased Activity in
754 Human Visual Cortex during Directed Attention in the Absence of Visual Stimulation. *Neuron*
755 22:751–761.
- 756 Kay K, Rokem A, Winawer J, Dougherty R, Wandell B (2013a) GLMdenoise: a fast, automated
757 technique for denoising task-based fMRI data. *Front Neurosci* 7:1–15.
- 758 Kay KN, Winawer J, Rokem A, Mezer A, Wandell BA (2013b) A two-stage cascade model of
759 BOLD responses in human visual cortex. *Diedrichsen J, ed. PLoS Comput Biol* 9:e1003079.
- 760 Kim YH, Gitelman DR, Nobre AC, Parrish TB, LaBar KS, Mesulam MM (1999) The large-scale
761 neural network for spatial attention displays multifunctional overlap but differential asym-
762 metry. *Neuroimage* 9:269–277.
- 763 Kincade JM, Abrams RA, Astafiev SV, Shulman GL, Corbetta M (2005) An event-related func-
764 tional magnetic resonance imaging study of voluntary and stimulus-driven orienting of atten-
765 tion. *Journal of Neuroscience* 25:4593–4604.
- 766 Kinchla, R. A. (1980). The measurement of attention. In R. S. Nickerson (Ed.), *Attention and per-
767 formance VIII*, 213-238.
- 768 Kinchla RA, Chen Z, Evert D (1995) Precue effects in visual search: data or resource limited?
769 *Perception & Psychophysics* 57:441–450.
- 770 Larsson J, Heeger DJ (2006) Two retinotopic visual areas in human lateral occipital cortex. *Jour-
771 nal of Neuroscience* 26:13128–13142.
- 772 Li X, Lu Z-L, Tjan BS, Doshier BA, Chu W (2008) Blood oxygenation level-dependent contrast
773 response functions identify mechanisms of covert attention in early visual areas. *Proc Natl
774 Acad Sci USA* 105:6202–6207.
- 775 Ling S, Carrasco M (2006a) Sustained and transient covert attention enhance the signal via dif-
776 ferent contrast response functions. *Vision Res* 46:1210–1220.
- 777 Ling S, Carrasco M (2006b) Sustained and transient covert attention enhance the signal via dif-
778 ferent contrast response functions. *Vision Res* 46:1210–1220.
- 779 Ling S, Carrasco M (2006c) When sustained attention impairs perception. *Nat Neurosci* 9:1243–
780 1245.
- 781 Liu T, Abrams J, Carrasco M (2009) Voluntary attention enhances contrast appearance. *Psycho-
782 logical Science* 20:354–362.
- 783 Liu T, Heeger DJ, Carrasco M (2006) Neural correlates of visual vertical meridian asymmetry. *J
784 Vis* 6:1294–1306.
- 785 Liu T, Larsson J, Carrasco M (2007a) Feature-based attention modulates orientation-selective
786 responses in human visual cortex. *Neuron* 55:313–323.
- 787 Liu T, Pestilli F, Carrasco M (2005) Transient attention enhances perceptual performance and
788 fMRI response in human visual cortex. *Neuron* 45:469–477.

- 789 Liu T, Stevens ST, Carrasco M (2007b) Comparing the time course and efficacy of spatial and
790 feature-based attention. *Vision Res* 47:108–113.
- 791 Lu Z-L, Li X, Tjan BS, Doshier BA, Chu W (2011) Attention Extracts Signal in External Noise: A
792 BOLD fMRI Study. *J Cogn Neurosci* 23:1148–1159.
- 793 Lu ZL, Doshier BA (1998) External noise distinguishes attention mechanisms. *Vision Res*
794 38:1183–1198.
- 795 Luck SJ, Hillyard SA, Mouloua M, Woldorff MG, Clark VP, Hawkins HL (1994) Effects of spatial
796 cuing on luminance detectability: psychophysical and electrophysiological evidence for early
797 selection. *Journal of Experimental Psychology: Human Perception and Performance* 20:887–
798 904.
- 799 Luo TZ, Maunsell JHR (2015) Neuronal Modulations in Visual Cortex Are Associated with Only
800 One of Multiple Components of Attention. *Neuron* 86:1182–1188.
- 801 Mackeben M, Nakayama K (1993) Express attentional shifts. *Vision Res* 33:85–90.
- 802 Mackey WE, Winawer J, Curtis CE (2017) Visual field map clusters in human frontoparietal cor-
803 tex. *Elife* 6:2704.
- 804 Martínez-Trujillo JC, Treue S (2002) Attentional Modulation Strength in Cortical Area MT De-
805 pends on Stimulus Contrast. *Neuron* 35:365–370.
- 806 Maunsell JHR, Cook EP (2002) The role of attention in visual processing. *Philosophical Trans-*
807 *actions of the Royal Society of London B: Biological Sciences* 357:1063–1072.
- 808 Mayer AR, Dorflinger JM, Rao SM, Seidenberg M (2004) Neural networks underlying endoge-
809 nous and exogenous visual–spatial orienting. *Neuroimage* 23:534–541.
- 810 McAdams CJ, Maunsell JHR (1999) Effects of Attention on Orientation-Tuning Functions of Sin-
811 gle Neurons in Macaque Cortical Area V4. *J Neurosci* 19:431–441.
- 812 McMains SA, Somers DC (2004) Multiple spotlights of attentional selection in human visual cor-
813 tex. *Neuron* 42:677–686.
- 814 Meyer KN, Du F, Parks E, Hopfinger JB (2018) Exogenous vs. endogenous attention: Shifting
815 the balance of fronto-parietal activity. *Neuropsychologia* 111:307–316.
- 816 Mitchell JF, Sundberg KA, Reynolds JH (2009) Spatial Attention Decorrelates Intrinsic Activity
817 Fluctuations in Macaque Area V4. *Neuron* 63:879–888.
- 818 Moerel D, Ling S, Jehee JFM (2016) Perceptual learning increases orientation sampling effi-
819 ciency. *Journal of Vision* 16:36–36.
- 820 Montagna B, Pestilli F, Carrasco M (2009) Attention trades off spatial acuity. *Vision Res* 49:735–
821 745.
- 822 Mulckhuysen M, Belopolsky AV, Heslenfeld D, Talsma D, Theeuwes J (2011) Distribution of at-
823 tention modulates salience signals in early visual cortex. Op de Beeck HP, ed. *PLoS ONE*
824 6:e20379.
- 825 Müller MM (2014) Neural Mechanisms of Feature-Based Attention. In: *Cognitive Electrophysiol-*
826 *ogy of Attention*, pp 123–135. Elsevier.

- 827 Müller NG, Ebeling D (2008) Attention-modulated activity in visual cortex—More than a simple
828 “spotlight.” *Neuroimage* 40:818–827.
- 829 Müller NG, Kleinschmidt A (2007) Temporal Dynamics of the Attentional Spotlight: Neuronal Cor-
830 relates of Attentional Capture and Inhibition of Return in Early Visual Cortex. *The Journal of*
831 *Cognitive Neuroscience* 19:587–593.
- 832 Murray SO (2008) The effects of spatial attention in early human visual cortex are stimulus inde-
833 pendent. *Journal of Vision* 8:1–11.
- 834 Nachmias J (1967) Effect of Exposure Duration on Visual Contrast Sensitivity with Square-Wave
835 Gratings. *J Opt Soc Am, JOA* 57:421–427.
- 836 Natale E, Marzi CA, Girelli M, Pavone EF, Pollmann S (2006) ERP and fMRI correlates of en-
837 dogenous and exogenous focusing of visual-spatial attention. *Eur J Neurosci* 23:2511–2521.
- 838 Nakayama K, Mackeben M (1989) Sustained and transient components of focal visual attention.
839 *Vision Res* 29:1631–1647.
- 840 Nobre AC, Coull JT, Maquet P, Frith CD, Vandenberghe R, Mesulam MM (2004a) Orienting at-
841 tention to locations in perceptual versus mental representations. *Cognitive Neuroscience,*
842 *Journal of* 16:363–373.
- 843 Nobre AC, Coull JT, Maquet P, Frith CD, Vandenberghe R, Mesulam MM (2004b) Orienting at-
844 tention to locations in perceptual versus mental representations. *Cognitive Neuroscience,*
845 *Journal of* 16:363–373.
- 846 O'Connor DH, Fukui MM, Pinsk MA (2002) Attention modulates responses in the human lateral
847 geniculate nucleus. *Nature* 5:1203–1209.
- 848 Ogawa S, Lee TM, Kay AR, Tank DW (1990) Brain magnetic resonance imaging with contrast
849 dependent on blood oxygenation. *Proc Natl Acad Sci USA* 87:9868–9872.
- 850 Peelen MV, Heslenfeld DJ, Theeuwes J (2004) Endogenous and exogenous attention shifts are
851 mediated by the same large-scale neural network. *Neuroimage* 22:822–830.
- 852 Pestilli F, Carrasco M (2005) Attention enhances contrast sensitivity at cued and impairs it at
853 uncued locations. *Vision Res* 45:1867–1875.
- 854 Pestilli F, Carrasco M, Heeger DJ, Gardner JL (2011) Attentional enhancement via selection and
855 pooling of early sensory responses in human visual cortex. *Neuron* 72:832–846.
- 856 Pestilli F, Ling S, Carrasco M (2009) A population-coding model of attention's influence on con-
857 trast response: Estimating neural effects from psychophysical data. *Vision Res* 49:1144–
858 1153.
- 859 Phillips WA (1974) On the distinction between sensory storage and short-term visual memory.
860 *Perception & Psychophysics* 16:283–290.
- 861 Poletti M, Rucci M, Carrasco M (2017) Selective attention within the foveola. *Nat Neurosci*
862 20:1413–1417.
- 863 Poltoratski S, Ling S, McCormack D, Tong F (2017) Characterizing the effects of feature salience
864 and top-down attention in the early visual system. *J Neurophysiol* 118:564–573.
- 865 Posner MI, Snyder CR, Davidson BJ (1980) Attention and the detection of signals. *J Exp Psychol*
866 109:160–174.

- 867 Reed AV (1973) Speed-Accuracy Trade-Off in Recognition Memory. *Science* 181:574–576.
- 868 Ress D, Backus BT, Heeger DJ (2000) Activity in primary visual cortex predicts performance in
869 a visual detection task. *Nat Neurosci* 3:940–945.
- 870 Reynolds JH, Heeger DJ (2009) The Normalization Model of Attention. *Neuron* 61:168–185.
- 871 Reynolds JH, Pasternak T, Desimone R (2000) Attention increases sensitivity of V4 neurons.
872 *Neuron* 26:703–714.
- 873 Rosen AC, Rao SM, Caffarra P, Scaglioni A, Bobholz JA, Woodley SJ, Hammeke TA, Cunning-
874 ham JM, Prieto TE, Binder JR (1999) Neural basis of endogenous and exogenous spatial
875 orienting. A functional MRI study. *Cognitive Neuroscience, Journal of* 11:135–152.
- 876 Ruff CC, Kristjánsson Á, Driver J (2007) Readout from iconic memory and selective spatial at-
877 tention involve similar neural processes. *Psychological Science* 18:901–909.
- 878 Ruff DA, Cohen MR (2014) Attention can either increase or decrease spike count correlations in
879 visual cortex. *Nat Neurosci* 17:1591–1597.
- 880 Seiss E, Driver J, Eimer M (2009) Effects of attentional filtering demands on preparatory ERPs
881 elicited in a spatial cueing task. *Clin Neurophysiol* 120:1087–1095.
- 882 Senoussi M, Moreland JC, Busch NA, Dugué L (2019) Attention explores space periodically at
883 the theta frequency. *Journal of Vision* 19:1–17.
- 884 Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Tootell R (1995)
885 Borders of multiple visual areas in humans revealed by functional magnetic resonance im-
886 aging. *Science* 268:889–893
- 887 Sergent C, Ruff CC, Barbot A, Driver J, Rees G (2011) Top-down modulation of human early
888 visual cortex after stimulus offset supports successful postcued report. *The Journal of Cog-
889 nitive Neuroscience* 23:1921–1934.
- 890 Sergent C, Wyart V, Babo-Rebelo M, Cohen L, Naccache L, Tallon-Baudry C (2013) Cueing
891 Attention after the Stimulus Is Gone Can Retrospectively Trigger Conscious Perception. *Cur-
892 rent Biology* 23:150–155.
- 893 Silvetti M, Lasaponara S, Lecce F, Dragone A, Macaluso E, Doricchi F (2015) The Response of
894 the Left Ventral Attentional System to Invalid Targets and its Implication for the Spatial Ne-
895 glect Syndrome: a Multivariate fMRI Investigation. *Cereb Cortex* 1–2.
- 896 Somers DC, Dale AM, Seiffert AE, Tootell RB (1999) Functional MRI reveals spatially specific
897 attentional modulation in human primary visual cortex. *PNAS* 96:1663–1668.
- 898 Sperling G, Melchner MJ (1978) The attention operating characteristic: examples from visual
899 search. *Science* 202:315–318.
- 900 Thibault L, van den Berg R, Cavanagh P, Sergent C (2016) Retrospective Attention Gates Dis-
901 crete Conscious Access to Past Sensory Stimuli. *PLoS ONE* 11:e0148504.
- 902 Wandell BA, Dumoulin SO, Brewer AA (2007) Visual field maps in human cortex. *Neuron* 56:366–
903 383.
- 904 Wang F, Chen M, Yan Y, Zhaoping L, Li W (2015) Modulation of Neuronal Responses by Exog-
905 enous Attention in Macaque Primary Visual Cortex. *Journal of Neuroscience* 35:13419–
906 13429.

- 907 Wang HX, Merriam EP, Freeman J, Heeger DJ (2014) Motion direction biases and decoding in
908 human visual cortex. *Journal of Neuroscience* 34:12601–12615.
- 909 Wickelgren WA (1977) Speed-accuracy tradeoff and information processing dynamics. *Acta Psy-*
910 *chologica* 41:67–85.
- 911 Williford T, Maunsell JHR (2006) Effects of Spatial Attention on Contrast Response Functions in
912 Macaque Area V4. *J Neurophysiol* 96:40–54.
- 913 Yashar A, Lamy D (2011) Refining the dual-stage account of intertrial feature priming: does motor
914 response or response feature matter? *Atten Percept Psychophys* 73:2160–2167.
- 915 Yeshurun Y, Carrasco M (1998) Attention improves or impairs visual performance by enhancing
916 spatial resolution. *Nature* 396:72–75.
- 917 Yeshurun Y, Montagna B, Carrasco M (2008) On the flexibility of sustained attention and its ef-
918 fects on a texture segmentation task. *Vision Research* 48:80–95.
- 919 Yeshurun Y, Rashal E (2010) Precueing attention to the target location diminishes crowding and
920 reduces the critical distance. *Journal of Vision* 10:16–16.