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2 **Covert spatial attention is uniform across cardinal meridians despite**
3 **differential adaptation**

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35 **Abstract**

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37 Visual adaptation and attention are two processes that help manage the brain's limited
38 bioenergetic resources for perception. Visual perception is heterogeneous around the visual field:
39 it is better along the horizontal than the vertical meridian (horizontal-vertical anisotropy, HVA),
40 and better along the lower than the upper vertical meridian (vertical meridian asymmetry, VMA).
41 Recently, we showed that visual adaptation is more pronounced at the horizontal than the vertical
42 meridian, but whether and how this differential adaptation modulates the effects of covert spatial
43 attention remains unknown. In this study, we investigated whether and how the effects of
44 endogenous (voluntary) and exogenous (involuntary) covert attention on an orientation
45 discrimination task vary at the cardinal meridians, with and without adaptation. We manipulated
46 endogenous (Experiment 1) or exogenous (Experiment 2) attention via an informative central or
47 uninformative peripheral cue, respectively. Results showed that (1) in the non-adapted condition,
48 the typical HVA and VMA emerged in contrast thresholds; (2) the adaptation effect was stronger
49 at the horizontal than the vertical meridian; and (3) regardless of adaptation, both endogenous
50 and exogenous attention enhanced and impaired performance at the attended and unattended
51 locations, respectively, to a similar degree at both cardinal meridians. Together, these findings
52 reveal that, despite differences between endogenous and exogenous attention, their effects
53 remain uniform across cardinal meridians—even under differential adaptation that reduces intrinsic
54 asymmetries of visual field representations.

55 **Keywords:** visual adaptation, endogenous attention, exogenous attention, visual performance
56 asymmetries, contrast sensitivity

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58 **Introduction**

59

60 Visual adaptation and attention are two processes that optimize performance and help manage
61 the brain's limited bioenergetic resources by allocating them according to task demands
62 (Carrasco, 2011; Lee, Fernández, & Carrasco, 2024; Lennie, 2003; Pestilli, Viera, & Carrasco,
63 2007). Although both processes modulate sensory responses, they have opposite effects on the
64 contrast response function. Visual adaptation helps manage bioenergetic resources by increasing
65 metabolic efficiency—it reduces sensitivity to repeated features and enhances sensitivity to novel
66 ones. For example, contrast adaptation can adjust the gain of the neural response so that its
67 dynamic range is matched to the range of levels in the stimulus (Boynton & Finney, 2003; Gardner
68 et al., 2005; Kohn, 2007; Perini, Cattaneo, Carrasco, & Schwarzbach, 2012; Vergeer, Mesik, Baek,
69 Wilmerding, & Engel, 2018; Webster, 2011, 2015). In contrast, visual attention selectively
70 improves information processing at an attended location while impairing processing elsewhere –
71 a ubiquitous performance tradeoff considered a push-pull mechanism (e.g., Dosher & Lu, 2000b;
72 Ling & Carrasco, 2006a; Pestilli & Carrasco, 2005; Pestilli, Ling, & Carrasco, 2009; Pestilli et al.,
73 2007; for reviews, Carrasco, 2011, 2014; Desimone & Duncan, 1995; Olivers, 2025).

74 There are two types of covert spatial attention: endogenous and exogenous. Endogenous
75 attention is voluntary, goal-driven, and flexible; exogenous attention is involuntary, stimulus-

76 driven, and automatic. Endogenous attention takes ~300 ms to be deployed and can be sustained
77 for many seconds, whereas exogenous attention peaks at ~120 ms and is transient (reviews:
78 Carrasco, 2011, 2014). Despite these differences, both types of attention improve performance
79 in many visual tasks, e.g., contrast sensitivity (e.g., Herrmann, Montaser-Kouhsari, Carrasco, &
80 Heeger, 2010; Pestilli et al., 2009), appearance (review: Carrasco & Barbot, 2019), and
81 orientation discrimination (e.g., Fernández, Okun, & Carrasco, 2022). However, they have distinct
82 effects in other tasks, e.g., texture segregation (e.g., Barbot & Carrasco, 2017; Jigo, Heeger, &
83 Carrasco, 2021; Yeshurun & Carrasco, 1998), and alter sensitivity across a different spatial
84 frequency range (Fernández et al., 2022; Jigo & Carrasco, 2020).

85 Exogenous attention restores contrast sensitivity after adaptation; although adaptation reduces
86 sensitivity, the magnitude of the exogenous attentional benefit at the attended location and its
87 concurrent cost at the unattended location remain comparable to those observed without
88 adaptation (Lee et al., 2024; Pestilli et al., 2007). However, whether and how endogenous
89 attention operates after adaptation is unknown. Thus, our first goal was to examine whether
90 endogenous attention restores contrast sensitivity after adaptation. It is possible that after
91 adaptation endogenous attention (1) enhances contrast sensitivity to a similar extent as without
92 adaptation, assuming that similar to exogenous attention (Lee et al., 2024; Pestilli et al., 2007),
93 endogenous attention and adaptation yield independent effects on contrast sensitivity (**Figure 1A**;
94 Hypothesis 1); (2) enhances sensitivity more than before adaptation, reflecting a compensatory
95 process given the flexible nature of endogenous attention, which optimizes performance as a
96 function of task demands (Barbot & Carrasco, 2017; Barbot, Landy, & Carrasco, 2012; Giordano,
97 McElree, & Carrasco, 2009; Hein, Rolke, & Ulrich, 2006; Yeshurun, Montagna, & Carrasco, 2008);
98 it may help more than without adaptation, as after decreases there is more room for improvement
99 (**Figure 1B**; Hypothesis 2); or (3) enhances sensitivity less than without adaptation; if reduced
100 baseline sensitivity limits the push-pull effects of endogenous attention (**Figure 1C**; Hypothesis
101 3).

102 Because endogenous attention is flexible (Barbot & Carrasco, 2017; Barbot et al., 2012; Giordano
103 et al., 2009; Hein et al., 2006; Yeshurun et al., 2008), but exogenous attention is not (Barbot et
104 al., 2012; Carrasco, Loula, & Ho, 2006; Crotty, Massa, Tellez, White, & Grubb, 2025; Giordano et
105 al., 2009; Hein et al., 2006; Luck & Thomas, 1999; Yantis & Jonides, 1996; Yeshurun & Carrasco,
106 1998), and because distinct brain regions are critical for their effect –right frontal eye fields for
107 endogenous attention (Fernández, Hanning, & Carrasco, 2023), and early visual cortex for
108 exogenous attention (Fernández & Carrasco, 2020; Lee et al., 2024), where it interacts with
109 adaptation (Lee et al., 2024) –it is possible that they exert different effects on contrast sensitivity
110 after adaptation. Therefore, our second goal was to determine whether endogenous and
111 exogenous attention have similar or different effects on contrast sensitivity following adaptation.

112 Finally, we investigated whether target location matters. In adult humans, visual performance is
113 better at the horizontal than the vertical meridian (horizontal-vertical anisotropy, HVA), and better
114 at the lower than the upper vertical meridian (vertical meridian asymmetry, VMA). These visual
115 field asymmetries, known as performance fields, are present in many fundamental visual tasks,
116 including contrast sensitivity (Abrams, Nizam, & Carrasco, 2012; Baldwin, Meese, & Baker, 2012;
117 Cameron, Tai, & Carrasco, 2002; Carrasco, Talgar, & Cameron, 2001; Corbett & Carrasco, 2011;
118 Fuller, Rodriguez, & Carrasco, 2008; Himmelberg, Winawer, & Carrasco, 2020; Lee & Carrasco,

119 2025; Purokayastha, Roberts, & Carrasco, 2021), visual acuity (Kwak, Hanning, & Carrasco, 2023;
120 Montaser-Kouhsari & Carrasco, 2009), spatial resolution (Altpeter, Mackeben, & Trauzettel-
121 Klosinski, 2000; Carrasco, Williams, & Yeshurun, 2002; Greenwood, Szinte, Sayim, & Cavanagh,
122 2017; Talgar & Carrasco, 2002), and motion (Fuller & Carrasco, 2009; Tünçok, Kiorpis, &
123 Carrasco, 2025), as well as mid-level visual processes, such as texture segregation (Barbot, Xue,
124 & Carrasco, 2021; Greenwood et al., 2017; Talgar & Carrasco, 2002; Z. Wang, Murai, & Whitney,
125 2020) and crowding (Greenwood et al., 2017; Kurzawski et al., 2023; Petrov & Meleshkevich,
126 2011), and high-level tasks, such as numerosity perception (Chakravarthi, Papadaki, & Krajnik,
127 2022), face perception (Afraz, Pashkam, & Cavanagh, 2010; Kim & Chong, 2024), word
128 identification (Tsai, Liao, Hou, Jang, & Chen, 2024), and visual short-term memory (Montaser-
129 Kouhsari & Carrasco, 2009).

130 These visual field asymmetries are resistant to endogenous (Purokayastha et al., 2021; Tünçok,
131 Carrasco, & Winawer, 2025) and exogenous attention (Cameron et al., 2002; Carrasco et al.,
132 2001; Roberts, Ashinoff, Castellanos, & Carrasco, 2018; Roberts, Cyberman, Smith, Kiorpis, &
133 Carrasco, 2016), as well as to temporal (Fernández, Denison, & Carrasco, 2019) attention. Thus,
134 performance fields are not easily reshaped. On the contrary, presaccadic attention, which
135 enhances the processing at the location of the impending saccade target, exacerbates
136 performance asymmetries at the cardinal locations by enhancing contrast sensitivity the most at
137 the horizontal meridian and the least at the upper vertical meridian (Hanning, Himmelberg, &
138 Carrasco, 2022, 2024; Kwak, Hanning, & Carrasco, in press; Kwak, Zhao, Lu, Hanning, &
139 Carrasco, 2024).

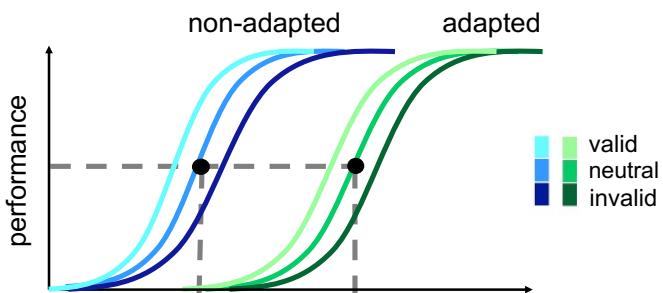
140 A recent study showed that visual adaptation is stronger at the horizontal than the vertical
141 meridian, leading to more homogeneous perception by mitigating the HVA (Lee & Carrasco, 2025).
142 It remains unknown, however, whether and how endogenous and exogenous attention reshape
143 performance fields after such differential adaptation. Thus, our third goal was to investigate
144 whether, following adaptation, covert spatial attention enhances contrast sensitivity (1) to the
145 same extent at the cardinal meridians around polar angle, similar to without adaptation (e.g.,
146 Carrasco et al., 2001; Purokayastha et al., 2021; Roberts et al., 2018; Roberts et al., 2016; Tünçok,
147 Carrasco, & Winawer, 2025) (**Figure 1D**; Hypothesis 4), (2) more at the vertical than the horizontal
148 meridian, and more at the upper than the lower vertical meridian, acting as a compensatory
149 mechanism to reduces asymmetries (**Figure 1E**; Hypothesis 5), or (3) more where baseline
150 performance is already better (i.e., the horizontal meridian) than where it is worse (i.e., vertical
151 meridian, especially the upper vertical meridian), thereby exaggerating asymmetries (**Figure 1F**;
152 Hypothesis 6).

153 Both adaptation (Altan, Morgan, Dakin, & Schwarzkopf, 2025; Dao, Lu, & Dosher, 2006; Gardner
154 et al., 2005; Perini et al., 2012; Pestilli et al., 2007) and endogenous attention (Dosher & Lu,
155 2000a; Ling & Carrasco, 2006a; Lu, Lesmes, & Dosher, 2002; Pestilli et al., 2009) primarily affect
156 the contrast gain of the contrast response function (**Figure 1A**), i.e., a shift in threshold, whereas
157 exogenous attention primarily affects response gain (Fernández & Carrasco, 2020; Pestilli et al.,
158 2009), i.e., a shift in asymptote. Additionally, according to a prominent normalization model of
159 attention (Reynolds & Heeger, 2009), exogenous attention can also affect contrast gain when the
160 attentional window is wider than the stimulus size, and endogenous attention can also affect
161 response gain when the attentional window is narrower than the stimulus size (Herrmann et al.,

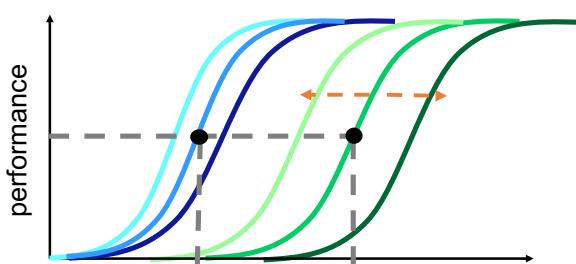
162 2010). In this study, to directly compare the two types of attention before and after adaptation at
 163 the cardinal meridians, we induced a larger attentional window in the exogenous attention
 164 experiment, enabling contrast gain effects predicted by Reynolds and Heeger's (2009)
 165 normalization model of attention.

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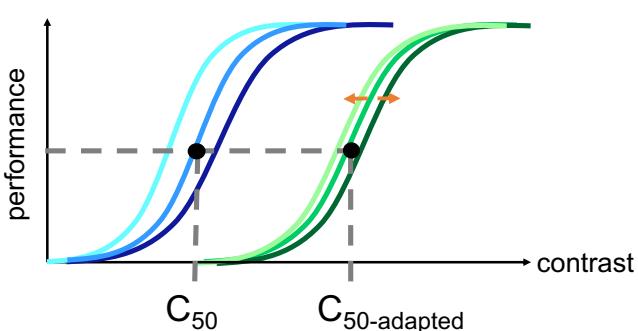
(A) Hypothesis 1



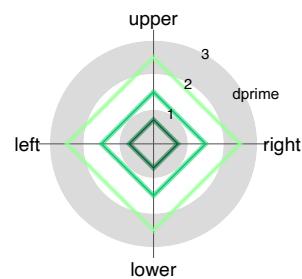
(B) Hypothesis 2



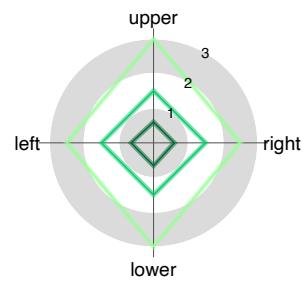
(C) Hypothesis 3



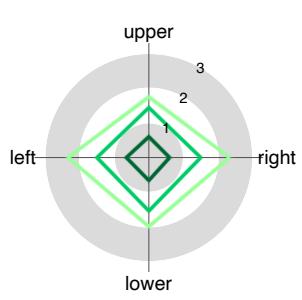
(D) Hypothesis 4



(E) Hypothesis 5



(F) Hypothesis 6



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169 Figure 1. (A-C) Hypotheses regarding effects on contrast sensitivity. (A) Hypothesis 1: Attentional effect is
 170 comparable with and without adaptation. The C_{50} and $C_{50\text{-adapted}}$ indicate the contrast threshold derived
 171 from the titration procedures in the non-adapted and adapted conditions, respectively. (B) Hypothesis 2:
 172 Attentional effect is larger with than without adaptation. (C) Hypothesis 3: Attentional effect is smaller than
 173 without adaptation. (D-F) Hypotheses regarding effects on contrast sensitivity as a function of location at
 174 the cardinal locations. (D) Hypothesis 4: Attentional effect is comparable around polar angle after adaptation.
 175 (E) Hypothesis 5: Attentional effect is stronger at the vertical than horizontal meridian. (F) Hypothesis 6:
 Attentional effect is smaller at the vertical than horizontal meridian.

176 In summary, we asked (1) whether and how endogenous attention restores contrast sensitivity
177 following adaptation, (2) whether endogenous and exogenous attention have similar or distinct
178 effects on contrast sensitivity before and after adaptation, and (3) whether these effects uniformly
179 or differentially across the cardinal meridians around the visual field. These findings are essential
180 for elucidating how the visual system engages adaptation and attention—two fundamental visual
181 processes that manage limited bioenergetic resources—to optimize performance across locations
182 that differ in intrinsic discriminability and in their corresponding representation in cortical surface
183 area.

184

185 **Experiment 1 – Endogenous attention**

186 **Methods**

187

188 **Participants**

189 Twelve adults (5 females, age range: 24-36 years old), including author HHL, participated in the
190 experiment. All of them had normal or corrected-to-normal vision. Sample size was based on
191 previous studies on adaptation (Lee et al., 2024), with an effect size of $d=1.3$, and on performance
192 fields (Lee & Carrasco, 2025), with an effect size of $d=1.41$ for performance in the neutral trials.
193 According to G*Power 3.0 (Faul, Erdfelder, Lang, & Buchner, 2007), we would need 9 participants
194 for adaptation and 8 participants for performance fields to reach a power=0.9. We also estimated
195 the required sample size for the interaction between adaptation and location, based on a recent
196 study between adaptation and performance fields (Lee & Carrasco, 2025) ($\eta_p^2=0.34$), by
197 assuming SD=1, we would need 10 subjects to reach a power=0.9 according to the Monte-Carlo
198 simulation (1,000 iterations per possible subject number). The Institutional Review Board at New
199 York University approved the experimental procedures, and all participants provided informed
200 consent before they started the experiment.

201 **Stimuli and apparatus**

202 The target Gabor (diameter = 4° , 5 cpd, 1.25° full-width at half maximum) was presented on the
203 left, right, upper and lower cardinal meridian locations (8° from the center to center). There were
204 four placeholders (length = 0.16° , width = 0.06°) 0.5° away from the Gabor's edge. The fixation
205 cross consisted of a plus sign (length = 0.25° ; width = 0.06°) at the center of the screen. The
206 endogenous attentional cue (length = 0.75° ; width = 0.2°) was presented at the center.

207 Participants were in a dimly lit, sound-attenuated room, with their head placed on a chinrest 57
208 cm away from the monitor. All stimuli were generated using MATLAB (MathWorks, MA, USA) and
209 the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) on a gamma-corrected 20-inch
210 ViewSonic G220fb CRT monitor with a spatial resolution of 1,280 x 960 pixels and a refresh rate
211 of 100 Hz. To ensure fixation, participants' eye movements were recorded using EYELINK 1000
212 (SR Research, Osgoode, Ontario, Canada) with a sample rate of 1,000 Hz.

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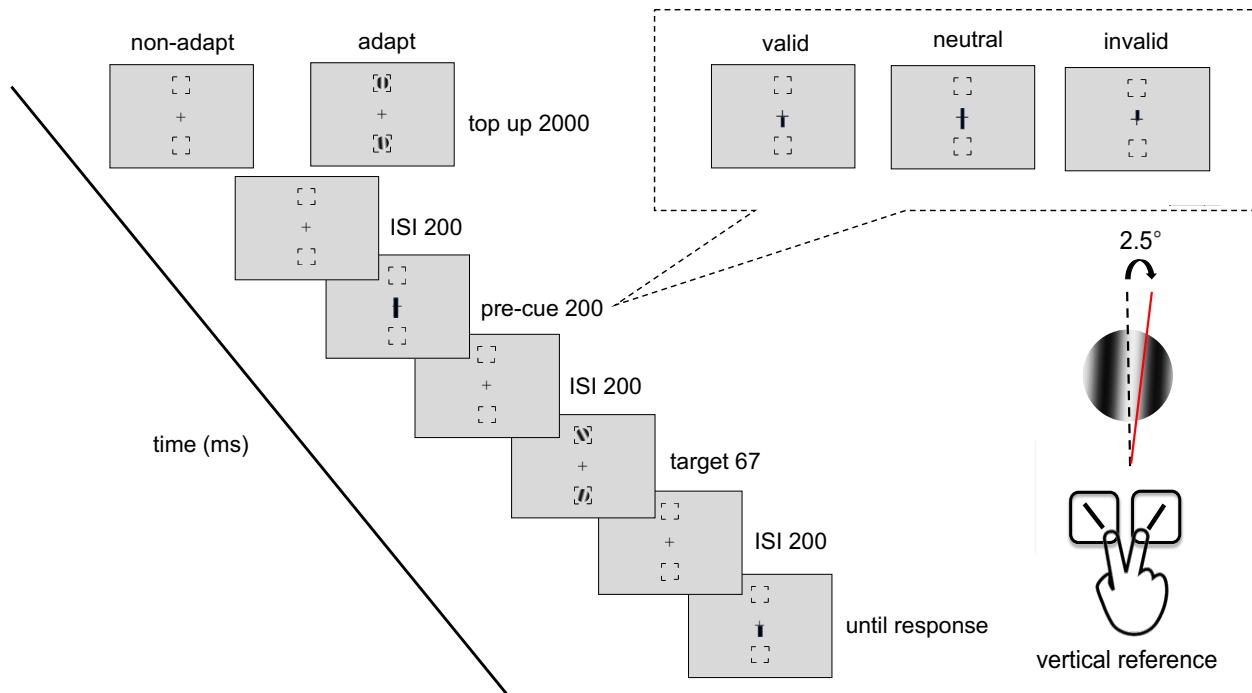
214 **Experimental design and procedures**

215 **Figure 2** shows the procedure of titration and the endogenous attention task. In the adapted
216 condition, at the beginning of each block, participants adapted to a vertical 5-cpd Gabor patch

217 flickering at 7.5 Hz in a counterphase manner, presented at the target location for 60 seconds.
218 Each trial started with a 2s top-up phase to ensure a continuous adaptation effect throughout the
219 block. In the non-adaptation condition, participants maintained fixation at the center for 4s (without
220 Gabor) at the beginning of each block and for 2s at the beginning of each trial.

221

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223
224 **Figure 2.** Experimental procedure: Participants performed either adaptation or nonadaptation blocks, each
225 in separate experimental sessions. The target Gabor stimulus was always presented within the black
226 placeholder, and target meridians were blocked. The target, two vertical Gabor stimuli were presented 8°
227 away from the center (e.g., at the vertical meridian here; at the horizontal meridian in a different block).
228 Participants were instructed to respond whether the Gabor was tilted clockwise or counterclockwise from
229 vertical. The pre-cue either matches (valid condition), mismatches (invalid condition) the response cue, or
230 does not provide location information (neutral condition). For illustration purposes, the stimulus size and
231 spatial frequency shown here are not to scale.

232

233 After the top-up, there was a 200 ms ISI before an endogenous pre-cue was presented for 100
234 ms. Following a 200-ms ISI the tilted Gabor was then presented for 67 ms, followed by another
235 200-ms ISI and then the response cue. In a valid trial, the location indicated by the response cue
236 matches the precue; in an invalid trial, they mismatch; in a neutral cue condition, the pre-cue
237 points at both locations. Participants had to judge whether the target Gabor was tilted clockwise
238 or counterclockwise off vertical. The tilt angle was 2.5°, based on pilot data and our previous study
239 (Lee & Carrasco, 2025), to ensure an adaptation effect while avoiding floor or ceiling performance.

240

241 A feedback tone was presented when participants gave an incorrect response. The target
242 locations were blocked in a horizontal block or a vertical block, where the target locations were
243 presented at the horizontal or vertical meridians, respectively. Participants were asked to respond

244 as accurately as possible while fixating at the center of the screen throughout the trial. A trial
245 would be interrupted and repeated at the end of the block if participants' eyes position deviated
246 $\geq 1.5^\circ$ from the center, from the pre-cue onset until the response cue onset.

247
248 Participants completed the adapted and non-adapted attentional task on the vertical and the
249 horizontal meridian on different days, with a counterbalanced order. The order of horizontal and
250 vertical meridian blocks was randomized, and the adaptation and non-adaptation titration were
251 implemented on different days, with a counterbalanced order. There were 4 independent
252 staircases for each adaptation condition and location, varying Gabor contrast from 2% to 85% to
253 reach $\sim 75\%$ accuracy for the orientation discrimination task. Each staircase started from 4
254 different points (85%, 2%, the median contrast of 43.5%, and a random point between 2% and
255 85%) and contained 48 trials. Four blocks (192 trials per location for each adaptation and non-
256 adaptation conditions) were conducted consecutively for the horizontal meridian block or the
257 vertical meridian block. The contrast threshold was derived using an adaptive staircase procedure
258 using the Palamedes toolbox (Prins & Kingdom, 2018), as in previous studies (e.g., Fernández &
259 Carrasco, 2020; Hanning et al., 2022; Jigo & Carrasco, 2018; Lee & Carrasco, 2025; Lee et al.,
260 2024) and averaging the last 8 trials. The Gabors were always preceded by a neutral pre-cue,
261 which, as in many studies (e.g., Dosher & Lu, 2000b; Fernández et al., 2022; Huang, Liao, Chen,
262 & Chen, 2025; Jigo & Carrasco, 2020; Li, Pan, & Carrasco, 2021; Luzardo & Yeshurun, 2025;
263 Palmieri & Carrasco, 2024; Ramamurthy, White, & Yeatman, 2024; Tünçok, Carrasco, & Winawer,
264 2025), provided the same temporal information as the valid and invalid cues, but no information
265 about the spatial location.
266

267 In this endogenous attention task, for each adapted and non-adapted condition, 20% of the trials
268 had a neutral cue, which pointed at both locations; 80% of the trials had an attentional cue pointing
269 toward a location, 75% among them were valid cues, and the other 25% were invalid cues. All
270 participants completed a practice session to familiarize themselves with the task procedure.
271

272 **Psychometric function fitting**

273 We fitted a Weibull function for the accuracy as a function of contrast threshold. For each location
274 and adaptation condition, a logistic function was fit to the data using maximum likelihood
275 estimation using the fmincon function in MATLAB. The results derived from the psychometric
276 function estimation positively correlated ($p < .01$) with the staircase results in all experiments,
277 verifying our procedure in all conditions.
278

279 **Behavioral data analyses**

280 Behavioral data analyses were performed using R (Team, 2000). A three-way repeated-measures
281 analysis of variance (ANOVA) on d' was conducted on the factors of location (horizontal meridian,
282 upper, lower), adaptation (adapted, non-adapted), and attention (valid, neutral, invalid) conditions
283 to assess statistical significance. Repeated-measures ANOVA along with effect size (η^2) were
284 computed in R and used to assess statistical significance.
285
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287

288 **Results**

289

290 **Adaptation effect varied around polar angle**

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292 After deriving the c_{50} contrast for the horizontal meridian (HM), upper, and lower vertical meridians
 293 for both the adapted and non-adapted conditions, we conducted a two-way ANOVA on contrast
 294 thresholds (**Figure 3**). This analysis showed a main effect of location [$F(2,22)=7.89$, $p=.003$,
 295 $\eta_p^2=0.42$] and a higher threshold in the adapted than non-adapted conditions [$F(1,11)=18.44$,
 296 $p=.001$, $\eta_p^2=0.63$], and an interaction [$F(2,22)=3.58$, $p=.045$, $\eta_p^2=0.25$], indicating that the
 297 adaptation effect varied across locations.

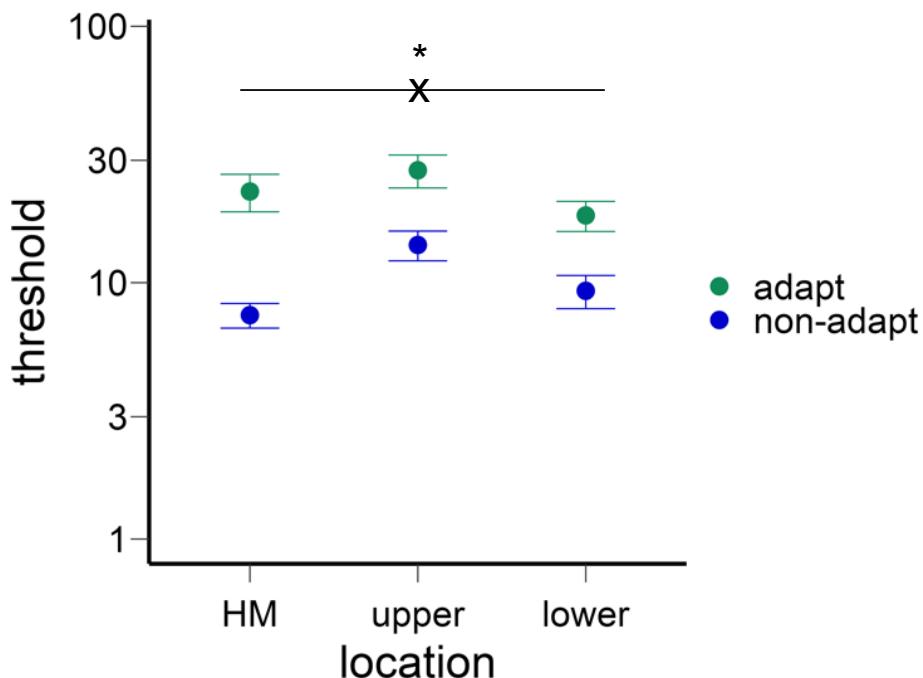
298

299 We confirmed that the HVA and VMA emerged in the non-adaptation condition (**Figure 3**):
 300 Contrast thresholds were lower along the horizontal than the vertical meridian [$t(11)=5.87$, $p<.001$,
 301 $d=1.69$] and lower at the lower than upper vertical meridian [$t(11)=2.37$, $p=.037$, $d=0.68$].

302

303 Next, we assessed the adaptation effect at the horizontal and vertical meridians. The normalized
 304 adaptation effect (calculated as the difference between adapted and non-adapted thresholds
 305 divided by the sum of the thresholds, as in Lee and Carrasco (2025) was stronger at the horizontal
 306 than the vertical meridian [$t(11)=3.39$, $p=.006$, $d=0.98$] (**Figure 3**, see gaps between adapt and
 307 non-adapt conditions for different locations), but no significant difference between the upper and
 308 lower vertical meridian [$t(11)<1$].

309



310

311 **Figure 3.** The contrast thresholds for different locations and adaptation conditions. The thresholds were
 312 higher in the vertical than horizontal meridian (HM), and higher in the upper than lower vertical meridian.
 313 The thresholds were also higher in the adapted than non-adapted conditions. Critically, the adaptation effect
 314 was stronger in the horizontal than vertical meridian. The error bars indicate ± 1 SEM.

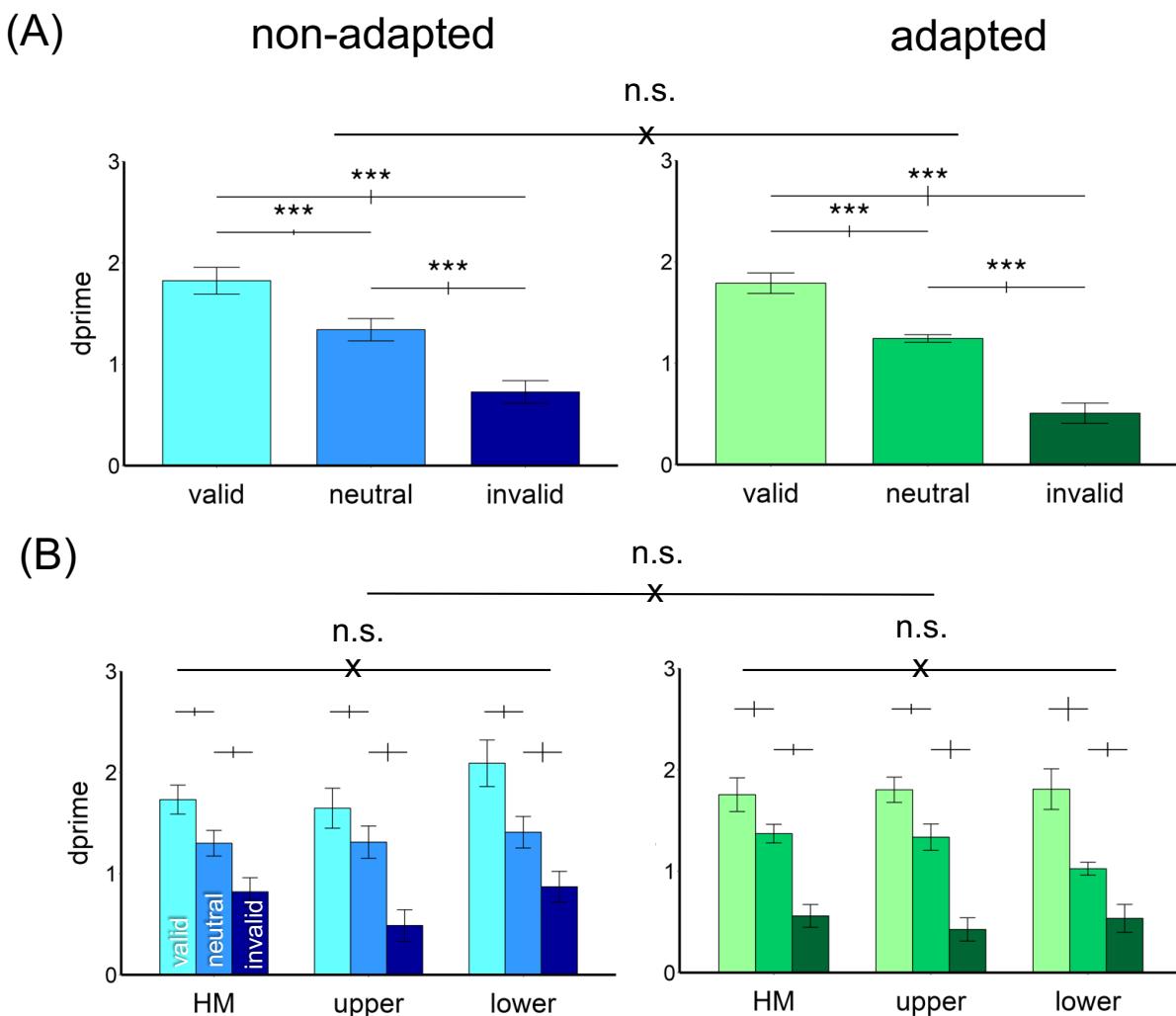
315 **Endogenous attentional effect**

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317 **Figure 4** shows the results. We compared the endogenous attentional effect on d' by conducting
 318 a three-way ANOVA on the factors of location (HM, upper, lower), attentional validity (valid,
 319 neutral, invalid), and adaptation (adaptation, non-adaptation). Given that we titrated the contrast
 320 thresholds across locations and adaptation conditions, we expected no main effects of either
 321 adaptation or location. Indeed, there was a main effect of attention [$F(2,22)=53.18, p<.001,$
 322 $\eta_p^2=0.83$], but neither of location [$F(2,22)<1$], nor of adaptation [$F(1,11)<1$]. There was neither a
 323 3-way interaction nor 2-way interactions [all $p>.1$].

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Figure 4. Performance in Experiment 1. (A) d' was higher in the valid followed by neutral and invalid conditions in both non-adapted and adapted conditions. There was no difference between the adapted and non-adapted conditions. (B) The attentional effects were similar around polar angle –horizontal meridian (HM), and upper and lower vertical meridian– and were comparable in the adapted and non-adapted conditions. The error bars above the bar plots indicate ± 1 SEM of the difference between conditions. *** $p<.001$, n.s. $p>.05$.

333 The results were further confirmed by separating the adapted and non-adapted conditions into
334 two 2-way ANOVAs on attention and location. For the non-adapted condition, we observed a main
335 effect of attention [$F(2,22)=46.74$, $p<.001$, $\eta_p^2=0.81$] but not of location [$F(2,22)<1$] or an
336 interaction [$F(4,44)=1.68$, $p>.1$]. The same pattern emerged for the adapted condition: a main
337 effect of attention [$F(2,22)=38.59$, $p<.001$, $\eta_p^2=0.78$] but not of location [$F(2,22)<1$] or an
338 interaction [$F(4,44)=1.48$, $p>.1$]. Thus, neither adaptation state nor location modulated the
339 pronounced overall effect of attention.

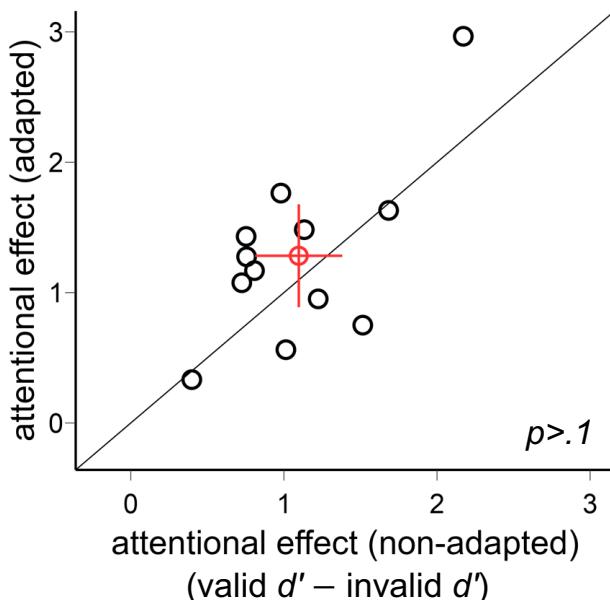
340

341 We plot the individual data for the endogenous attentional effect (valid d' – invalid d') in the
342 adapted and non-adapted conditions (**Figure 5**). There was no difference between the two
343 conditions [$t(11)=1.27$, $p>.1$].

344

345 In sum, the endogenous attentional effect was comparable across locations and adaptation
346 conditions.

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348

349 **Figure 5.** Comparison of the endogenous attentional effects (valid d' – invalid d') in Experiment 1. The
350 attentional effects were comparable in the adapted and non-adapted conditions. The red circle indicates
351 the mean of all participants, and the error bars indicate ± 1 SEM.

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353

354 **Experiment 2 — Exogenous attention**

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356 Experiment 1 shows that endogenous attention does not reshape the performance fields, even
357 after differential adaptation effects across meridians. In Experiment 2, we examined whether
358 exogenous attention exhibits a similar or distinct pattern as endogenous attention, given their well-
359 established differences in temporal dynamics: Whereas endogenous attention takes about 300
360 ms to deploy and its effects can be sustained for many seconds, exogenous attention effects peak

361 at about 120 ms and its effects are transient (reviews: Carrasco, 2011, 2014; Carrasco & Barbot,
362 2014). Moreover, endogenous attention is flexible whereas exogenous attention is not (e.g.,
363 Barbot & Carrasco, 2017; Barbot et al., 2012; Giordano et al., 2009; Hein et al., 2006; Nakayama
364 & Mackeben, 1989; Yantis & Jonides, 1996; Yeshurun & Carrasco, 1998, 2008), and the effects
365 of endogenous attention scale with cue validity, whereas those of exogenous attention do not
366 (e.g., Giordano et al., 2009; Kinchla, 1980; Mangun & Hillyard, 1990; Sperling & Melchner, 1978).
367

368 To manipulate exogenous attention, we used a peripheral cue (a bolded placeholder) presented
369 before the target onset. According to a normalization model of attention, exogenous attention can
370 also affect contrast gain when the attentional window is large enough (Reynolds & Heeger, 2009;
371 Herrmann et al., 2010). To induce a large attentional window while maintaining overlap between
372 the target and adaptors and ensure the adaptation effect, we randomly presented the target in
373 one of the five locations within the placeholders (**Figure 6**), and participants were explicitly
374 instructed to attend to the whole space encompassed by the placeholder, as the target could
375 appear anywhere within the placeholder. This procedure has been successfully used to
376 manipulate the size of the attentional window in both exogenous and endogenous covert spatial
377 attention, as well as in presaccadic attention (e.g., Binda & Murray, 2015; Cutrone, Heeger, &
378 Carrasco, 2018; Feng & Spence, 2017; Grubb et al., 2013; Herrmann et al., 2010; Li et al., 2021).
379

380 **Methods**

381

382 **Participants**

383 Eleven out of 12 participants¹ who participated in Experiment 1, including author HHL, also
384 participated in Experiment 2. We tested the same group of participants to compare the results
385 from endogenous and exogenous attentional effects after adaptation.

386

387 **Stimuli and apparatus**

388 **Figure 6** shows an experimental trial. The target stimuli and the apparatus were the same as
389 Experiment 1. The placeholders in Experiment 2 (length = 0.256° for placeholders that were
390 further away from the center, length = 0.192° for placeholders that were closer to the center, all
391 width = 0.06°) were larger, given that there were 5 possible target locations: center and 2° on the
392 upper, lower, left, or right of the central Gabor. During the cue presentation, the placeholders
393 became thicker (6 pixels bigger for the frame elements closer to the center and 8 pixels bigger for
394 the frame elements further away from the center) to capture participants' exogenous attention.
395

396

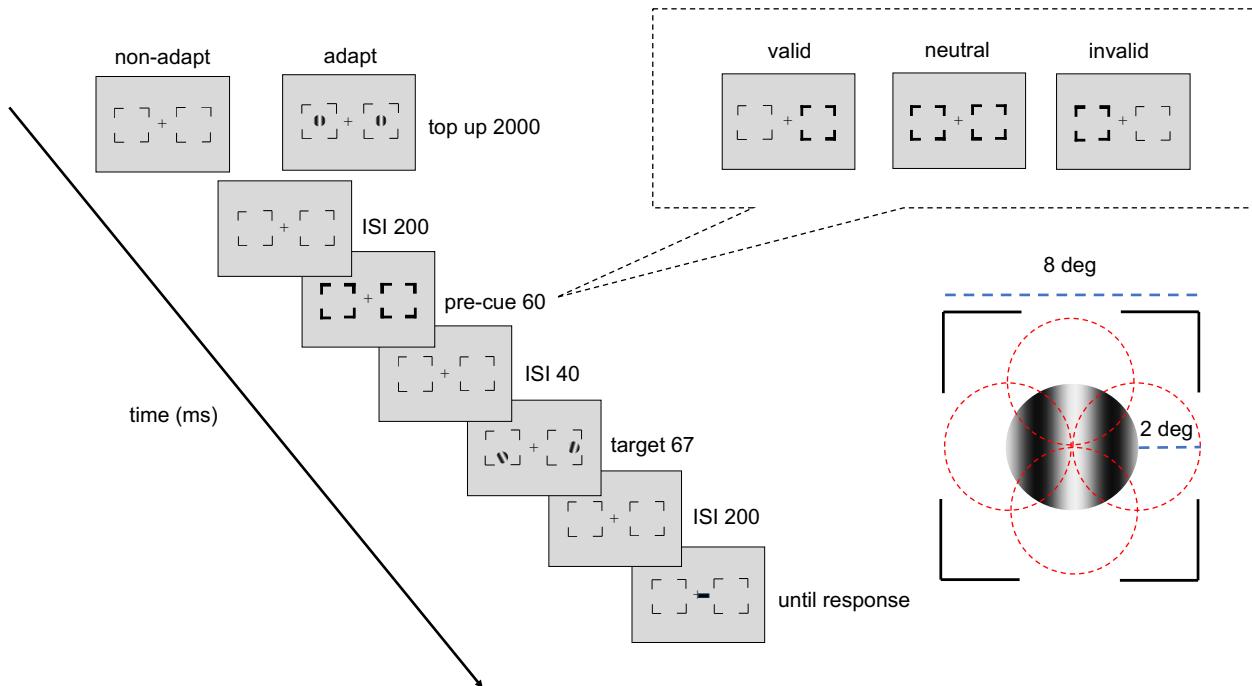
397 **Experimental design and procedures**

398

399 The same c_{50} contrast derived from Experiment 1 was used in Experiment 2 for the adapted and
400 non-adapted conditions across locations. The experimental design and procedures were the
401 same as in Experiment 1, except for the following: After the top-up, there was a 200-ms ISI before
402 the exogenous pre-cue appeared for 60 ms, followed by 40-ms ISI. The tilted Gabor was then
403 presented for 67 ms followed by another 200-ms ISI and the response cue. Participants were

¹ One participant was no longer around NYC to participate

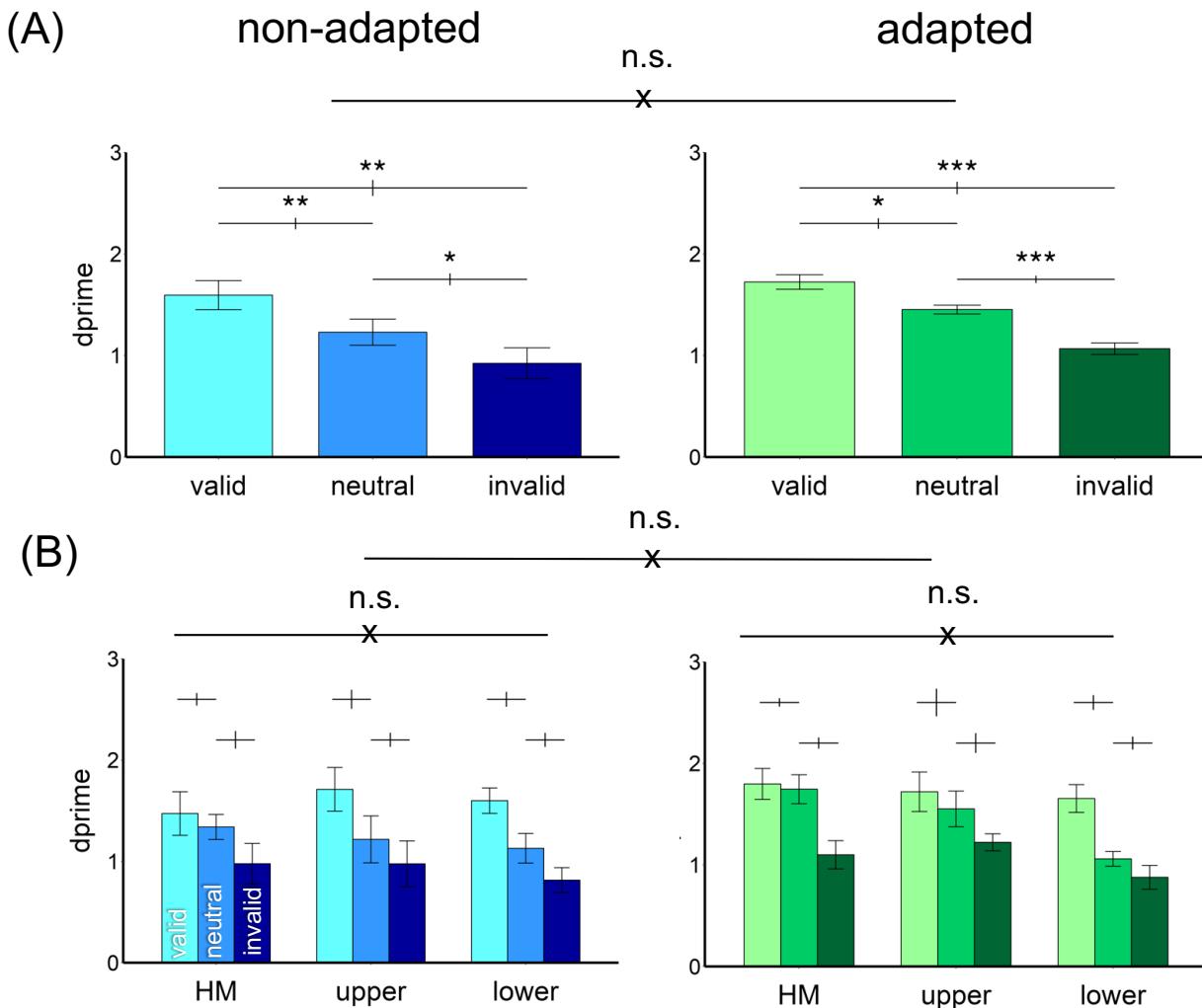
403 explicitly told that the exogenous cues were not informative; i.e., they were equally likely to be
 404 valid, neutral and invalid (33% each). Participants were instructed to enlarge their attentional
 405 window during the task, as they were explicitly told that the target could appear anywhere within
 406 the placeholders.
 407



408
 409
 410 **Figure 6.** Experimental procedure: The procedure was the same as Experiment 1 except for the pre-cue
 411 and ISI timings. The pre-cue (bolded placeholders) either matches (valid condition), mismatches (invalid
 412 condition) the response cue, or does not provide location information (neutral condition). The placeholders
 413 were wider (8°) than Experiment 1. The target, two vertical Gabor stimuli were presented on average 8°
 414 away from the center (e.g., at the horizontal meridian for example here; at the vertical meridian in a different
 415 block). There were 5 possible target locations, which were 2° away from the central Gabor. For illustration
 416 purposes, the stimulus size and spatial frequency shown here are not to scale.
 417
 418

419 Results

420
 421 **Figure 7** shows our results. As in Experiment 1, we compared the exogenous attentional effect
 422 on d' by conducting a three-way ANOVA on the factors of location (HM, upper, lower), attentional
 423 validity (valid, neutral, invalid), and adaptation (adaptation, non-adaptation). There was a main
 424 effect of attention [$F(2,20)=20.7, p<.001, \eta_p^2=0.67$], but neither of location [$F(2,20)=2.61, p=.099$],
 425 nor of adaptation [$F(1,10)=1.08, p>.1$]. There was neither a 3-way interaction [$F(4,40)=2.36, p=.069$] nor 2-way interactions [all $p>.1$].
 426
 427



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Figure 7. Performance in Experiment 2. (A) d' was higher in the valid followed by neutral and invalid conditions in both non-adapted and adapted conditions. There was no difference between the adapted and non-adapted conditions. (B) The attentional effects were similar around polar angle –horizontal meridian (HM), and upper and lower vertical meridian– and were comparable in the adapted and non-adapted conditions. The error bars above the bar plots indicate ± 1 SEM of the difference between conditions. ***
 $p < .001$, ** $p < .01$, * $p < .05$, n.s. $p > .05$.

435
436

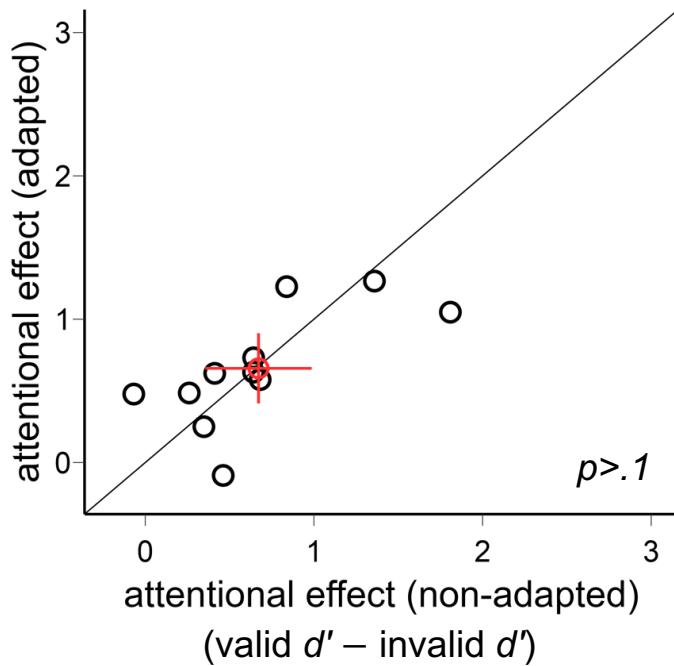
437 The results here were further confirmed by separating the adapted and non-adapted conditions
438 into two 2-way ANOVAs on attention and location. For the non-adapted condition, we observed a
439 main effect of attention [$F(2,20)=13.33, p < .001, \eta_p^2=0.57$] but neither of location [$F(2,20)<1$], nor
440 an interaction [$F(4,40)=1.33, p > .1$]. The same pattern emerged for the adapted condition: a main
441 effect of attention [$F(2,20)=21.19, p < .001, \eta_p^2=0.68$] but neither of location [$F(2,20)=2.33, p > .1$]
442 nor an interaction [$F(4,40)=2.01, p > .1$].
443

444 We plot the individual data for the exogenous attentional effect (valid d' – invalid d') in the adapted
445 and non-adapted conditions (**Figure 8**). There was no difference between the two conditions
446 [$t(10)<1$].

447

448 In sum, the exogenous attentional effect was comparable across locations and adaptation
449 conditions.

450



451
452 **Figure 8.** Comparison of the exogenous attentional effects (valid d' – invalid d') in Experiment 2. The
453 attentional effects were comparable in the adapted and non-adapted conditions. The red circle indicates
454 the mean of all participants, and the error bars indicate ± 1 SEM.

455

456

457 Comparing Experiments 1 and 2

458

459 Given that we had 11 common participants in Experiments 1 and 2, we conducted a 4-way
460 repeated-measures within-subject ANOVA on the factor of type of attention (endogenous,
461 exogenous), attentional validity (valid, neutral, invalid), adaptation (adapted, non-adapted), and
462 location (HM, upper, lower). There was a main effect of attentional validity [$F(2,20)=51.72, p<.001$,
463 $\eta_p^2=0.84$], and an interaction between attentional validity and type of attention [$F(2,20)=7.38$,
464 $p=.004, \eta_p^2=0.42$]. Post-hoc analyses indicated that valid condition had the highest d' followed by
465 neutral [valid – neutral: $t(10)=6.78, p<.001, d=2.04$] and invalid conditions [neutral – invalid:
466 $t(10)=6.17, p<.001, d=1.86$]. The attentional effect (valid d' – invalid d') was stronger for
467 endogenous than exogenous attention [$t(10)=2.95, p=.015, d=0.89$]. Importantly, there were no
468 4-way interaction [$F(4,40)<1$] nor any other significant effects [all $p>.05$], indicating that the effect
469 for both types of attention did not vary across locations nor across adaptation conditions.

470
471 Furthermore, we found a positive Pearson correlation [$r=.39, p=.025$] between the exogenous and
472 endogenous overall attentional effect (collapsing across adaptation conditions and locations),
473 which indicates that those observers who had a stronger effect of one type of attention also had
474 a stronger effect for the other type.

475
476

477 Discussion

478

479 In this study, we investigated whether attention interacts with adaptation around polar angle. Our
480 results are consistent with separate studies showing: (1) without adaptation, the typical
481 performance fields emerged, with lower contrast thresholds at the horizontal than the vertical
482 meridian (HVA) and at the lower than the upper vertical meridian (VMA) (e.g., Abrams et al., 2012;
483 Baldwin et al., 2012; Cameron et al., 2002; Carrasco et al., 2001; Corbett & Carrasco, 2011; Fuller
484 et al., 2008; Himmelberg et al., 2020; Lee & Carrasco, 2025); (2) adaptation effects were stronger
485 at the horizontal than the vertical meridian (Lee & Carrasco, 2025); and (3) both endogenous
486 attention (Purokayastha et al., 2021; Tünçok, Carrasco, & Winawer, 2025) and exogenous
487 attention (Cameron et al., 2002; Carrasco et al., 2001; Roberts et al., 2018; Roberts et al., 2016)
488 enhanced contrast sensitivity similarly across all tested locations. Furthermore, our results
489 revealed that: (1) endogenous attention restored contrast sensitivity following adaptation, (2)
490 endogenous and exogenous attention had similar effects on contrast sensitivity before and after
491 adaptation—both enhanced contrast sensitivity at the attended location, with concomitant costs at
492 unattended locations, and (3) they did so uniformly at the cardinal meridians around the visual
493 field—despite differential adaptation effects.

494

495 The finding that endogenous attention enhances contrast sensitivity to a similar extent in adapted
496 and non-adapted conditions indicates that visual adaptation does not modulate the attentional
497 effect. This novel finding is consistent with corresponding findings for exogenous attention on
498 contrast sensitivity after adaptation (Lee et al., 2024; Pestilli et al., 2007). Despite its flexible
499 nature (reviews: Carrasco, 2011, 2014; Carrasco & Barbot, 2014; Olivers, 2025), endogenous
500 attention neither increased nor decreased contrast sensitivity differentially before and after
501 adaptation, indicating that these two processes, which help manage limited bioenergetic
502 resources, play independent roles in shaping performance.

503

504 Typically, the effect of exogenous attention manifests as response gain and the effect of
505 endogenous attention as contrast gain (Ling & Carrasco, 2006a; Pestilli et al., 2009). In the
506 exogenous attention experiment, we induced contrast gain by manipulating the size of the
507 attentional window, presenting the target Gabor at one of 5 different locations within a larger
508 stimulus placeholder. According to Reynolds and Heeger's normalization model of attention,
509 attention produces contrast gain rather than response gain when the attentional window is large
510 relative to stimulus size (Reynolds & Heeger, 2009), a prediction confirmed psychophysically and
511 with functional magnetic resonance imaging (fMRI) (Herrmann et al., 2010). By contrast,
512 endogenous attention can induce response gain when deployed over a relatively smaller
513 attentional window than the stimulus size (Fernández et al., 2023; Herrmann et al., 2010; Morrone,

514 Denti, & Spinelli, 2004). Consistent with previous findings (Lee et al., 2024; Pestilli et al., 2007),
515 exogenous attention modulated contrast sensitivity to a similar extent in adapted and non-adapted
516 conditions, indicating that adaptation did not modulate its effect. These results support Hypothesis
517 1: after adaptation, covert spatial attention modulates contrast sensitivity to the same extent as
518 without adaptation (**Figure 1A**).
519

520 In this exogenous attention experiment, to induce a larger attentional window, participants were
521 explicitly told that the target could appear anywhere within the placeholders. This manipulation
522 should not affect the effects of exogenous attention as it cannot induce endogenous attention.
523 The effects of endogenous attention scale with cue validity (e.g., Giordano et al., 2009; Kinchla,
524 1980; Mangun & Hillyard, 1990; Sperling & Melchner, 1978), and in the exogenous attention
525 experiment, the cue was uninformative: each of the valid, invalid, and neutral cues was presented
526 on 33% of the trials, so when a cue indicated one location out of two, its validity was 50%. Thus,
527 had observers deployed endogenous attention in Experiment 2, performance would have been
528 similar for valid and invalid conditions. Instead, we found significant benefits at the attended
529 location and significant costs at unattended locations, consistent with an exogenous attention
530 effect. Moreover, given the timing of the exogenous cue (~120 ms)—and that endogenous
531 attention takes ~300 ms to be deployed (e.g., Cheal, Lyon, & Hubbard, 1991; Geweke, Pokta, &
532 Störmer, 2021; Liu, Stevens, & Carrasco, 2007; Nakayama & Mackeben, 1989; Remington,
533 Johnston, & Yantis, 1992, for reviews, see Carrasco 2011, 2014, Carrasco & Barbot, 2015)—
534 endogenous attention could not contribute.
535

536 Adaptation was more pronounced at the horizontal than the vertical meridian. Unlike our previous
537 study (Lee & Carrasco, 2025), which blocked each target location, here we introduced greater
538 target uncertainty by using two possible target locations per trial (**Figure 2**). The replication of the
539 adaptation pattern across studies shows that that the previous findings are robust to target
540 uncertainty and generalize across participants. Most adaptation studies have examined only the
541 horizontal meridian (e.g., Beaton & Blakemore, 1981; Carrasco et al., 2006; Gao, Webster, &
542 Jiang, 2019; Greenlee, Georgeson, Magnussen, & Harris, 1991; Pestilli et al., 2007; Schieting &
543 Spillmann, 1987), only the vertical meridian (e.g., Bell, Gheorghiu, Hess, & Kingdom, 2011; Bell,
544 Gheorghiu, & Kingdom, 2009; Montaser-Kouhsari & Rajimehr, 2004), or did not analyze target
545 locations separately (e.g., Bao, Fast, Mesik, & Engel, 2013; Lin, Zhou, Naya, Gardner, & Sun,
546 2021; Ling & Carrasco, 2006b; Zimmermann, Weidner, Abdollahi, & Fink, 2016). Our results add
547 further evidence that adaptation differs across meridians, an important finding to consider in future
548 studies and models of vision.
549

550 Endogenous and exogenous attention enhanced contrast sensitivity similarly around polar angle,
551 despite the differential effects of adaptation. Consistent with previous studies (Cameron et al.,
552 2002; Carrasco et al., 2001; Roberts et al., 2018; Roberts et al., 2016), asymmetries at the
553 cardinal locations were resistant to both endogenous and exogenous attention, indicating their
554 resilient nature and that they cannot be easily reshaped. In contrast, consistent with a recent
555 finding (Lee & Carrasco, 2025), visual adaptation reduced contrast sensitivity more at the
556 horizontal than the vertical meridian, yet neither type of covert spatial attention modulated the
557 extent of the asymmetries altering the shape of the performance fields, notwithstanding the

558 differential adaptation effect. This similar effect is notable given that endogenous attention is
559 flexible and exogenous attention automatic (e.g., Carrasco, 2011, 2014; Carrasco & Barbot, 2014;
560 Olivers, 2025), yet neither compensated for poor performance. These findings provide further
561 evidence regarding the resilience of polar angle asymmetries and support Hypothesis 4 (**Figure**
562 **1D**): visual adaptation does not modulate the effects of covert spatial attention, even at the
563 location of poorest performance.

564

565 What contributes to performance asymmetries in the HVA and VMA? These asymmetries arise
566 from both retinal and cortical factors. Retinally, cone density is higher at the horizontal than the
567 vertical meridian (Curcio, Sloan Jr, Packer, Hendrickson, & Kalina, 1987; Curcio, Sloan, Kalina,
568 & Hendrickson, 1990), and midget-RGC density is higher at the lower than the upper vertical
569 meridian (Curcio et al., 1990; Song, Chui, Zhong, Elsner, & Burns, 2011). Cortically, V1 surface
570 area is larger for the horizontal than the vertical meridian, and for the lower than the upper vertical
571 meridian (Benson, Kupers, Barbot, Carrasco, & Winawer, 2021; Himmelberg et al., 2021;
572 Himmelberg, Kwak, Carrasco, & Winawer, 2025; Himmelberg, Tünçok, et al., 2023; Himmelberg,
573 Winawer, & Carrasco, 2022, 2023; Lee & Carrasco, 2025; Silva et al., 2018). Moreover, cortical
574 factors account for more variance in these asymmetries than retinal factors (Kupers, Benson,
575 Carrasco, & Winawer, 2022). Still, these factors cannot fully explain behavioral differences
576 observed in psychophysical tasks, which are diminished but still present once stimulus size is
577 cortically magnified (Jigo, Tavdy, Himmelberg, & Carrasco, 2023), suggesting that additional
578 factors –such as sensory tuning and neuronal computations– also contribute to the HVA and VMA
579 (Himmelberg, Winawer, & Carrasco, 2023; Jigo et al., 2023; Xue, Barbot, Abrams, Chen, &
580 Carrasco, 2025).

581

582 Endogenous and exogenous attention rely on different neural substrates. fMRI studies show
583 differential activity modulation across the frontoparietal network (Beck & Kastner, 2014;
584 Buschman & Miller, 2009; Chica, Bartolomeo, & Lupiáñez, 2013; Fiebelkorn & Kastner, 2020;
585 Kastner & Buschman, 2017; Meyer, Du, Parks, & Hopfinger, 2018), temporoparietal junction
586 (Dugué, Merriam, Heeger, & Carrasco, 2018), and visual cortex (Dugué, Merriam, Heeger, &
587 Carrasco, 2020; Hopfinger & West, 2006; Ling, Jehee, & Pestilli, 2015). Transcranial magnetic
588 stimulation (TMS) studies, which disrupt the neuronal balance between excitation and inhibition
589 (Bradley, Nydam, Dux, & Mattingley, 2022; Kobayashi & Pascual-Leone, 2003; Valero-Cabré,
590 Pascual-Leone, & Coubard, 2011), revealed that early visual cortex plays a critical role for
591 adaptation (Lee et al., 2024; Perini et al., 2012) and exogenous attention (Fernández & Carrasco,
592 2020; Lee et al., 2024), whereas the human homologue of the right frontal eye fields (rFEF+)
593 plays a critical role for endogenous attention (Fernández et al., 2023). Critically, disrupting rFEF+
594 does not affect exogenous attention (Chen et al., 2025), and disrupting early visual cortex does
595 not affect endogenous attention (Fernández et al., 2023), indicating a double dissociation. Despite
596 these distinct neural underpinnings, both types of covert spatial attention affected contrast
597 sensitivity uniformly at the cardinal meridians around polar angle and did not interact with location
598 or adaptation. These findings suggest that distinct neuronal populations underlie polar angle
599 asymmetries, adaptation, and attentional modulation.

600

601 We found stronger attentional effects for endogenous than exogenous attention. Given that
602 adaptation is more effective when the adaptor and the target spatially overlap (Kovács, Zimmer,
603 Harza, & Vidnyánszky, 2007; Larsson & Harrison, 2015; Webster, 2011, 2015), we introduced
604 target uncertainty with 5 possible target locations and allowed 2° overlap between adaptor and
605 target to elicit adaptation while allowing exogenous attention to operate via contrast gain. This
606 manipulation may have yielded a slightly narrower exogenous attentional window than for
607 endogenous attention in our design, as well as compared with previous studies. For example,
608 Herrmann et al. (2010) used five possible target locations with no overlap, whereas in our current
609 study the target Gabors could overlap by 2° within placeholders. According to Reynolds and
610 Heeger's normalization model of attention (Reynolds & Heeger, 2009), attention multiplies
611 stimulus-evoked activity before divisive normalization. In our task, normalization may have pooled
612 a broader suppressive drive than in typical exogenous attention tasks, but not as broad as in
613 typical endogenous attention tasks —leading to less pronounced contrast gain and thus weaker
614 exogenous than endogenous attention effects.

615

616 Why do type of spatial covert attention, adaptation, and polar angle asymmetries not interact?
617 The visual cortex plays a crucial role in all three processes. fMRI studies have shown that covert
618 endogenous spatial attention modulates activity in visual cortex via feedback from frontoparietal
619 cortex (Buschman & Miller, 2009; Chica et al., 2013; Corbetta, Patel, & Shulman, 2008; Corbetta
620 & Shulman, 2002; Dugué et al., 2020; Lauritzen, D'Esposito, Heeger, & Silver, 2009; Pestilli,
621 Carrasco, Heeger, & Gardner, 2011) and increasingly modulates activity in the occipital visual
622 areas (Dugué et al., 2020), with V1/V2, its early visual areas, being not critical for endogenous
623 attention, as TMS on these areas does not alter its effect on visual perception (Fernández et al.,
624 2023). In contrast, exogenous attention modulates visual cortex via feedforward activation
625 (Dassanayake, Michie, & Fulham, 2016; Dugué et al., 2020; Hopfinger, Luck, & Hillyard, 2004;
626 Liu, Pestilli, & Carrasco, 2005; F. Wang, Chen, Yan, Zhaoping, & Li, 2015; Westerberg, Schall,
627 Woodman, & Maier, 2023), and V1/V2 are critical for its effect, as TMS on these areas eliminates
628 the effect of exogenous attention on visual perception (Fernández & Carrasco, 2020; Lee et al.,
629 2024). Moreover, these two attention types also differentially modulate visual subregions of the
630 temporoparietal-junction (Dugué et al., 2018). All these differences underscore the distinct
631 contributions of endogenous and exogenous in modulating visual perception.

632

633 Early visual cortex also plays a critical role in visual adaptation. TMS over V1/V2 decreases
634 contrast adaptation (Perini et al., 2012), and adaptation modulates contrast response functions in
635 V1/V2 (Altan et al., 2025; Gardner et al., 2005; Vinke, Bloem, & Ling, 2022). A TMS study revealed
636 that adaptation and exogenous attention interact in early visual cortex (Lee et al., 2024), but it is
637 unknown whether they do so systematically around polar angle, as several factors shape
638 asymmetries. Moreover, it is presently unknown whether endogenous attention and adaptation
639 interact either in early occipital or in frontal areas.

640

641 Both adaptation (Lee & Carrasco, 2025) and polar angle asymmetries (Benson et al., 2021;
642 Himmelberg et al., 2022; Himmelberg, Winawer, & Carrasco, 2023; Lee & Carrasco, 2025)
643 correlate with V1 surface area, but surface area alone cannot fully account for these asymmetries
644 (Jigo et al., 2023). Additional factors such as neural gain also contribute to these asymmetries

645 (Xue et al., 2025). Future research integrating computational modeling, neuroimaging,
646 neurostimulation, and psychophysics will be essential to assess the relative contributions of
647 cortical and computational factors to attention, adaptation and polar angle asymmetries.

648
649 In conclusion, this study reveals that performance asymmetries are resistant to the effects of both
650 endogenous and exogenous covert spatial attention, despite their distinct temporal dynamics and
651 differences in flexibility—even after adaptation induces differential effects across meridians.
652 Although both adaptation and attention help allocate limited resources according to task demands,
653 neither type of covert spatial attention differentially enhance target processing at locations that
654 differ in intrinsic discriminability and their corresponding representation in cortical surface area.
655
656

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662
663

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