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1 The fate of non-selected activity in  
2 saccadic decisions: distinct goal-related  
3 and history-related modulation.

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15  
16 **ABBREVIATED TITLE:**

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17 The fate of non-selected activity

## 27 **1 ABSTRACT**

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28 *The Global Effect (GE) traditionally refers to the tendency of effectors (e.g. hand, eyes) to first land in*  
29 *between two nearby stimuli – forming a unimodal distribution. By measuring a shift of this distribution,*  
30 *recent studies used the GE to assess the presence of decision-related inputs on the motor map for eye*  
31 *movements. However, this method cannot distinguish whether one stimulus is inhibited or the other is*  
32 *facilitated and could not detect situations where both stimuli are inhibited or facilitated.*

33 *Here, we detect deviations in the bimodal distribution of landing positions for remote stimuli, and find*  
34 *that this bimodal GE reveals the presence, location and polarity (facilitation or inhibition) of history-*  
35 *related and goal-related modulation of the non-selected activity (e.g. the distractor activity in correct*  
36 *trials, and the target activity in error trials). We tested, for different inter-stimulus distances, the effect*  
37 *of the rarity of double-stimulus trials, and the difference between performing a discrimination task*  
38 *compared to free choice.*

39 *Our work shows that the effect of rarity is symmetric and decreases with inter-stimulus distances, while*  
40 *the effect of goal-directed discrimination is asymmetric – occurring only when the distractor is selected*  
41 *for the saccade – and maintained across inter-stimulus distances. These results suggest that the former*  
42 *effect changes the response property of the motor map, while the latter specifically facilitates the target*  
43 *location.*

44

## 45 **2 NEW & NOTEWORTHY:**

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46 *Deviations in landing positions for saccades to targets and distractors reveal the presence, location and*  
47 *polarity of history-related or goal-related signals.*

48 *Goal-directed discrimination appears to facilitate the target location, rather than inhibiting the*  
49 *distractor location,*

50 *Rare occurrence of a choice appears to indiscriminately increase the neural response for both locations.*

### 51 **3 INTRODUCTION**

---

52 No matter how efficient a decision-making system, its expression will ultimately be limited by the  
53 mechanisms used to translate decisions into actions. Those mechanisms can be seen as an encryption  
54 key to decipher decision-related signals from motor responses (e.g. eye or hand movement  
55 trajectories). In the context of saccadic eye movements, the Superior Colliculus (SC) is a key motor  
56 interface (a role shared with the Frontal Eye Field), integrating several sources of input to produce  
57 motor signals guiding the eye trajectories (for eye trajectories and SC activity, see, for instance,  
58 Goossens & van Opstal, 2012; White & Munoz, 2011 for a review on SC).

59 To model the saccadic motor interface it is common to use a race-to-threshold mechanism allied with  
60 a winner-take-all policy (Kopecz 1995; Kopecz and Schöner 1995; Trappenberg et al. 2001; Bompas  
61 and Sumner 2011, 2015, Satel et al. 2011, 2014; Wang et al. 2011; Marino et al. 2012). In these  
62 models, the race-winner both triggers (in time) and selects the destination for the next saccade;  
63 ‘when’ and ‘where’ are tightly coupled. Although these modelling efforts help us deduce the temporal  
64 dynamics of decision-related signals, they have not focused on the details of spatial selection (Wang  
65 et al. 2012a). In short, these models are optimized to explain only one side of the coin.

66 In other models the ‘where’ and ‘when’ processes are more loosely coupled (Findlay and Walker  
67 1999; Arai and Keller 2004; Wilimzig et al. 2006). This low coupling is twofold: 1) the ‘where’  
68 processes are not necessarily completed when the ‘when’ processes trigger a saccade; 2) all the  
69 activity present on the motor map is taken into account to generate the ‘where to move’ motor  
70 response (except in Findlay & Walker, 1999). The first idea can be illustrated with the saccadic  
71 curvature literature, where the incomplete interplay between target and distractor signals changes  
72 with saccade latency to produce curvature either towards or away from the distractor (McPeck et al.  
73 2003; McSorley 2006). The second point was demonstrated by observing the SC/FEF activity during  
74 saccade curvature (McPeck et al. 2003; McPeck 2006) or by reconstructing saccade trajectories from  
75 activity recorded in the SC (Goossens and Van Opstal 2006). Finally, the low coupling between ‘when’  
76 and ‘where’ is in line with recent results suggesting there is no winner-take-all in the SC motor  
77 interface in mice (Phongphanphane et al. 2014). The rationale, then, is that using a model of spatial  
78 interactions with a low coupling between ‘where’ and ‘when’ as a decryption key, saccade metrics  
79 can be used to characterize specific decision-related signals projecting onto the SC.

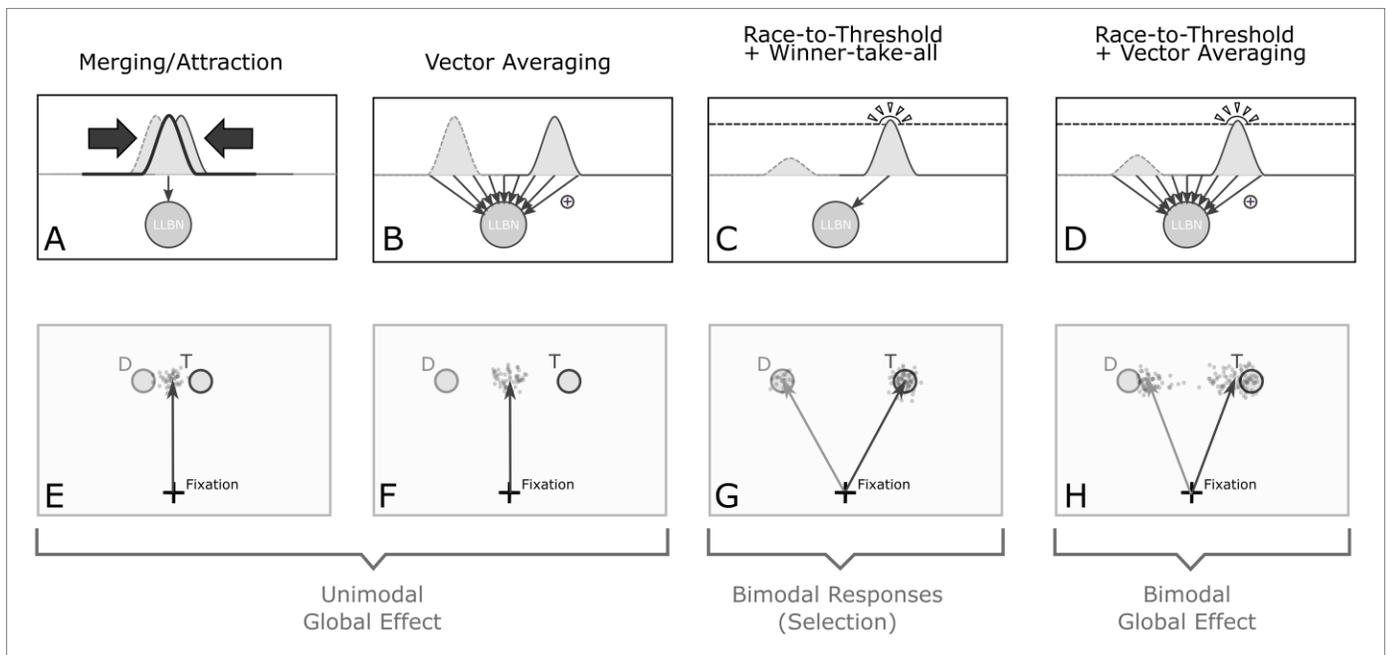
80 When two close visual stimuli are presented simultaneously, eye movements directed to one of them  
81 tend to land in between the two stimuli, betraying a spatial interaction (Findlay 1982; the Global

82 Effect, Deubel et al. 1984; see also Sailer et al. 2002 for hand movements), illustrated in Figure 1E,F.  
83 This Global Effect (GE) has been the topic of intensive investigation in the eye movement community  
84 to understand how visual stimuli interact in, or upstream of, the saccadic motor interface (Casteau  
85 and Vitu 2012; Tandonnet et al. 2012; Tandonnet and Vitu 2013; Van der Stigchel and Nijboer 2013).  
86 Two main accounts for the GE have been suggested (reviewed in the discussion of Katnani and  
87 Gandhi 2011) and they mainly differ in the order of their operations: the averaging mechanism and  
88 the transformation from SC space to visual/saccadic space.

89 The first account, which is compatible with winner-take-all models, assumes a merging mechanism  
90 driven by a specific pattern of lateral interactions in the SC (short range excitation, long range  
91 inhibition). Regions of activity induced by two *close* stimuli would merge into a single zone of activity  
92 located between them, as illustrated in Figure 1A/E (Arai et al. 1994; Kopecz and Schöner 1995;  
93 Wilimzig et al. 2006). To apply a winner-take-all in this case is equivalent to taking the average  
94 position between stimuli in SC space and then project the result to saccadic/visual space. Thus the  
95 landing positions of saccades would form a straight line in SC space, and an outward C-curve in the  
96 visual space (for a more detailed explanation, see Katnani and Gandhi 2011).

97 The second account suggests that vector averaging occurs when the population activity of the SC is  
98 decoded into a command for the extra-ocular muscles. Regions of activity of any two stimulations  
99 would *not* merge; the mechanism downstream would simply program the saccade corresponding to  
100 the average of all the saccadic vectors activated in the SC (Lee et al. 1988; Goossens and Van Opstal  
101 2005; Van Opstal and Goossens 2008; Gandhi and Katnani 2011; Katnani et al. 2012), as illustrated  
102 in Figure 1B/F. Note that this vector averaging mechanism has also been used to explain trajectory  
103 curvatures in hand and eye movements (Tipper et al. 1997; McSorley et al. 2004; Walton et al. 2005).  
104 Here, the averaging is applied directly on the saccadic vectors, which means that the average happens  
105 in visual/saccadic space. Thus the landing positions of the saccades would form a straight line in  
106 visual space and an inward C-curve in SC space (for a more detailed explanation, see Katnani and  
107 Gandhi 2011).

108



109

110 **Figure 1: Schematic of different mechanisms that could be involved in the spatial decision process. On the**  
 111 **top row, we represent different mechanisms that have been proposed for the saccadic motor map or**  
 112 **downstream machinery. The dark-edged and bright-edged curves stand for the activity of the target and**  
 113 **distractor, respectively. The horizontal dashed line represents a hypothetical saccade initiation threshold. On the**  
 114 **bottom row, we represent the effect of those mechanisms on saccade direction. The arrows represented the**  
 115 **average saccadic vector for each distribution mode while the dots draw the distribution of the saccade**  
 116 **endpoints. The bright-edged and dark-edged disks represent, respectively the distractor and the target on the**  
 117 **monitor screen. The black cross is the fixation stimulus. Panel A/E present the merging mechanism proposed to**  
 118 **explain the unimodal Global Effect. We highlight that this mechanism works on stimuli that are close enough for**  
 119 **their activity to overlap. Panel B/F show the vector averaging mechanism – where the overall activity on the**  
 120 **motor map is integrated by the Long Lead Burst Neurons (LLBN, dark-edged disk) – that has also been suggested**  
 121 **to explain the unimodal Global Effect. We highlight that it would work on remote stimuli. Panel C/G represent a**  
 122 **race-to-threshold mechanism that triggers and generates the saccade corresponding to the first point of activity**  
 123 **to reach the threshold on the motor map. In Panel D/H we suggest that a combination of the race-to-threshold**  
 124 **mechanism (C) and vector averaging (B) would lead to a bimodal Global Effect (see text for more details).**

125

126 When two simultaneous visual stimuli are remote rather than close, the landing position of the  
 127 saccades tends to form a bimodal distribution. Such bimodal distribution can be explained by a race-  
 128 to-threshold model combined with a winner-take-all mechanism (**Figure 1C/G**). In such a model, the  
 129 first zone to reach threshold would simply trigger an eye movement to the corresponding stimulus,  
 130 as illustrated in Figure 1C. As this system only retains the race winner, this would mean saccades are  
 131 directed either to one stimulus or the other; in such models the losing stimulus could affect the  
 132 latency (e.g. via lateral inhibition) but not the final destination of the action (Figure 1G).

133 However, while the GE traditionally refers to circumstances in which a unimodal distribution of  
 134 landing positions is observed between two relatively close stimuli (“genuine global effect”, Van der

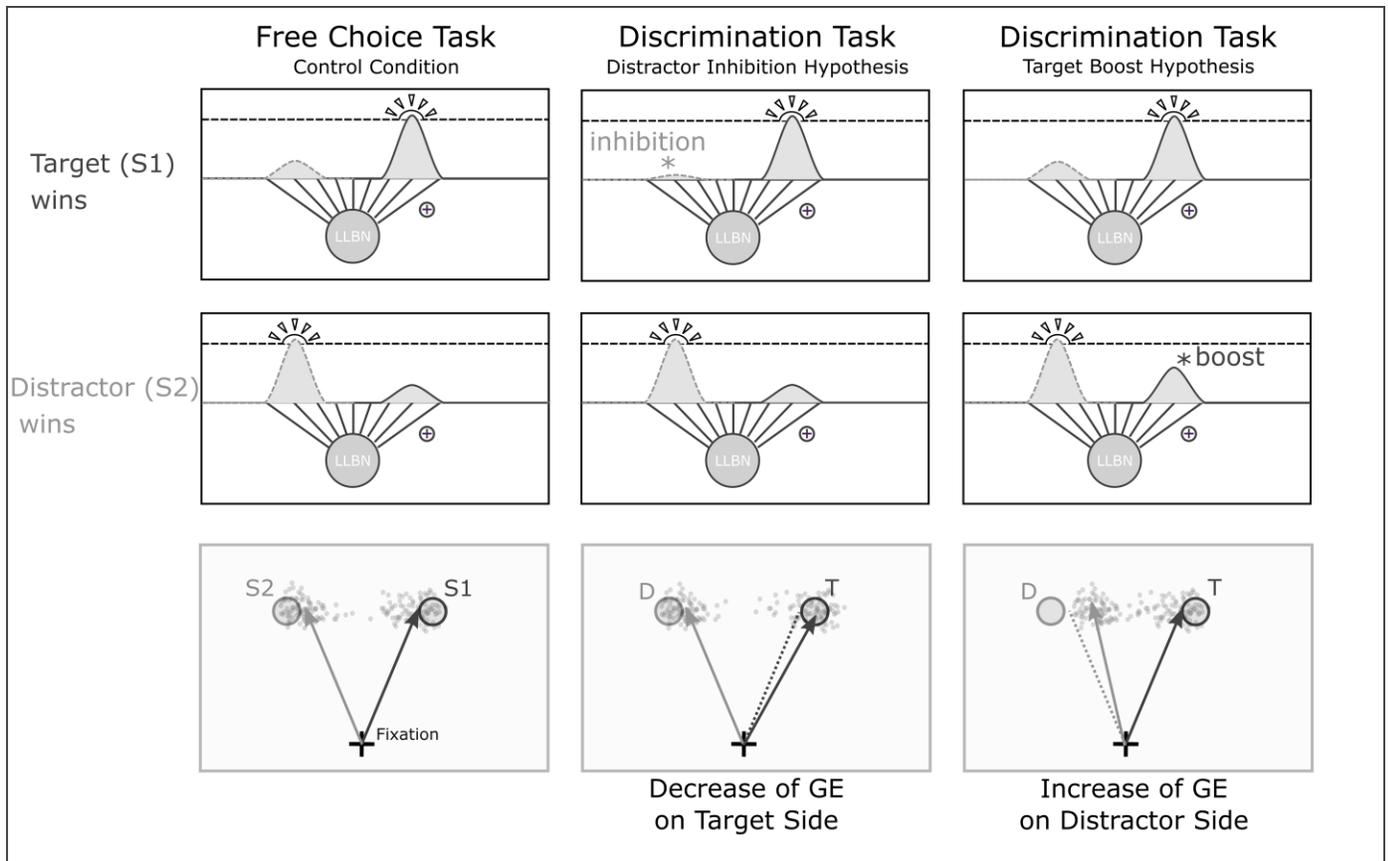
135 Stigchel and Nijboer 2013), there are indications that spatial interactions continue to occur for  
136 bimodal distributions when stimuli are further apart (Arai et al. 2004; Van der Stigchel et al. 2011).  
137 More evidence can be found in the saccade curvature literature in which a correlation between the  
138 initial directions and the landing positions of the saccades was reported (Van der Stigchel et al. 2007)  
139 for inter-stimulus distances that do not evoke unimodal GE. Based on this evidence, it seems that,  
140 even when saccades appear to be successfully directed to one stimulus or another, and do not land  
141 half way in between, close examination of the endpoints reveals some attraction or repulsion to/from  
142 the other stimulus (Figure 1H). This phenomenon, which we will refer to as the bimodal GE, could be  
143 explained neither by a merging nor by a vector averaging mechanism taken alone. The first aim of  
144 our article is to confirm and characterize the bimodal GE, and propose a simple model that can  
145 account for it.

146 This 'bimodal GE' could be explained by a model that features a low coupling between 'when' and  
147 'where' to move. It would combine a race-to-threshold mechanism, which triggers the saccade, with  
148 a vector averaging mechanism specifying the spatial destination (**Figure 1D**). Such a model is similar  
149 to that of Arai and Keller (2004) or Wilimzig et al. (2006). It would have to feature relatively low  
150 mutual inhibition so that the race loser maintains some activity at saccade onset (such as in McPeck  
151 et al. 2003) to influence the saccade metrics through the vector averaging (Figure 1D, and such as in  
152 Goossens and Van Opstal 2005; Van Opstal and Goossens 2008), predicting small deviations of the  
153 endpoints towards the losing stimulus (Figure 1H). This simple model predicts that such deviations  
154 ought to lie on a straight line in visual space and an inward curve in SC space, given that they are not  
155 occurring through merging within the SC.

156 If the bimodal GE is robust and our logic holds that it reflects residual activity for the *loser* in an  
157 incomplete decision process, then systematic modulation in bimodal GE should reflect the strength  
158 of this losing activity. This activity should change over time, being stronger at earlier points in the  
159 decision process. It has often been suggested that the relative importance of non-specific signals and  
160 discriminatory signals changes with latency, such that early inaccurate responses are relatively more  
161 driven by non-specific transient visual responses in the SC/FEF drive, while later more accurate  
162 responses are more driven by slower signals carrying more task-relevant information (Bompas and  
163 Sumner 2011, 2015; see also Boehnke and Munoz 2008; Schall et al. 2011). Heeman et al. (2014)  
164 found this relationship in the unimodal GE in a discrimination task: smaller GE was associated with  
165 longer latency. Our conceptual model for the bimodal GE predicts this same relationship: larger GE  
166 should be associated with shorter latency when the decision process is least complete.

167 Once we establish that the bimodal GE is systematically modulated in a way consistent with changing  
168 activity for the losing action option, it becomes a means to test aspects of theory that could not be  
169 tested with the unimodal GE, such as whether distractors are inhibited or targets facilitated during  
170 target selection. This can be achieved in a straightforward paradigm where the participant starts a  
171 trial by fixating a fixation cross and is instructed to make a saccade to peripheral stimuli as soon as  
172 they are presented. Single stimulus trials, in which only one peripheral stimulus is presented, are  
173 interleaved with double stimulus trials, in which two peripheral stimuli are presented. In the latter  
174 condition, the participant faces a choice situation (section 4.3 describes our paradigm in more detail).  
175 The type and context of the double stimulus trials can then be manipulated to assess how endpoint  
176 deviations at distractor and target locations are affected differently by endogenous signals.

177 Two types of endogenous signals can be fundamentally distinguished: goal-related and history-  
178 related (Awh et al. 2012). In the traditional GE paradigm, goal-related signals have been probed by  
179 comparing a discrimination task to a free choice condition – i.e. whether one stimulus is designated  
180 a target, or saccades to either stimulus are allowed. Although early studies failed to demonstrate goal-  
181 related effects (Ottens et al. 1985), more recent evidence clearly shows it (Heeman et al. 2014) while  
182 some clinical studies used it to probe the role of FEF in shaping the target discrimination signal (Van  
183 der Stigchel et al. 2013). Note that Heeman et al. (2014)'s results were predicted by the  
184 aforementioned model of Wilimzig et al. (2006), which features a low coupling between 'where' and  
185 'when' to move. However, the unimodal GE could not distinguish whether goal-related signals  
186 enhance the target or inhibit the distractor. This is also difficult to distinguish in term of latencies,  
187 where global slowing due to mutual inhibition, slower perceptual discrimination or increased  
188 caution could mask or interact with any facilitation or inhibition effects on target and distractor  
189 individually. With the bimodal GE, the distinction should be clearer: target enhancement would  
190 manifest as increased GE for saccades to the distractor (i.e. when the target *loses* the race), while  
191 inhibiting the distractor would diminish GE on saccades to the target (when the distractor loses the  
192 race; see **Figure 2**).



193

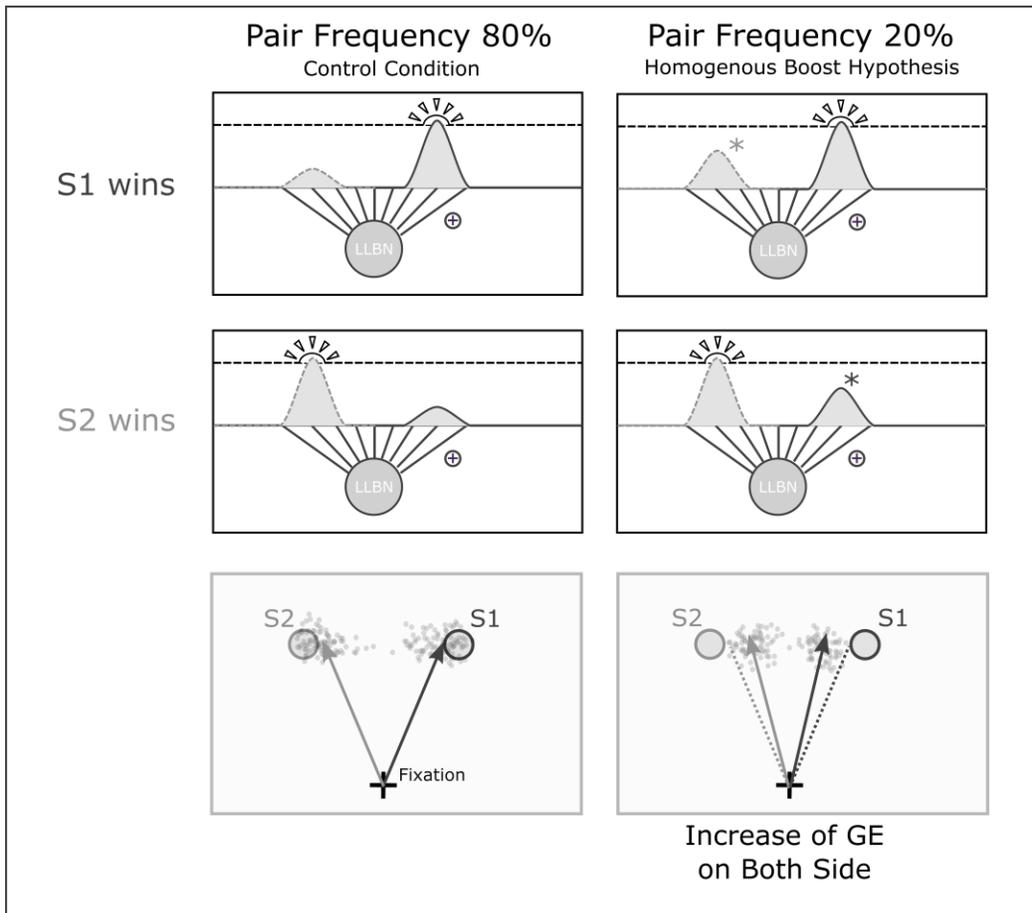
194 **Figure 2: Hypotheses for the Effect of Discrimination Task.** Rows 1 and 2 depict the activity for the target  
 195 and the distractor (dark and bright curves, respectively) on the motor map when one of them reaches the  
 196 threshold to trigger a saccade. Row 3 shows the predicted distributions of saccade endpoints. The participant is  
 197 presented with a pair of similar stimuli and is either required to make a saccade to the target and ignore the  
 198 distractor (discrimination condition), or is able to freely select one of them to make a saccade (free choice  
 199 condition; for consistency, we call one stimulus the target and one the distractor in all conditions). In free choice  
 200 (Column 1), we expect the bimodal Global Effect will be similar on S1 and S2 side, since the participant should  
 201 treat them as equivalent (Row 1). In the discrimination task, we expect the target stimulus to be relatively  
 202 advantaged, and thus the pattern may not be symmetrical. Under the assumption that the distractor is inhibited  
 203 while the discrimination progresses (Column 2), the activity of a loser distractor (Row 1) would be less than that  
 204 of a loser target (Row 2), leading to less bimodal GE on Target side – as compared with free choice (Row 3, dark  
 205 dashed line). Under the assumption that the target is boosted (Column 3), we would predict an opposite pattern  
 206 (Row 1 & 2), and the bimodal GE on the Distractor side would be larger compared to free choice (Row 3, bright  
 207 dashed line).

208

209 History-related signals, such as the spatial probability of the target, are also known to affect the GE  
 210 (He and Kowler 1989; Wang et al. 2012b). However, history-related signals that are spatially  
 211 nonspecific –such as the probability of occurrence of double-stimulus trials – would affect equally  
 212 both stimuli and could not be detected with the unimodal GE. Thus, their effect is unknown. When  
 213 comparing a condition with rare double-stimulus trials to a condition with frequent double-stimulus  
 214 trials, we hypothesized that rarity of double-stimulus trials could make both stimuli more salient,

215 leading to an increase of the bimodal GE for saccades to both stimuli (see **Figure 3**). Alternative  
 216 hypotheses would be no effect for spatially non-specific history, or an enhancement for frequent  
 217 conditions as occurs for spatially specific history effects.

218 Finally, because the bimodal GE can be measured over a large range of inter-stimulus distances, we  
 219 expect that it can be used to assess the spatial properties of the above signals. Specifically, we aimed  
 220 to investigate whether the effect of probability (or relative surprise) is similar to goal-related signals  
 221 (and at the same time, we explore which distance is best to study the bimodal GE).



222  
 223 **Figure 3: Hypothesis for the effect of Rarity.** Row 1 and 2 depict the stimulus-related activity on the motor  
 224 map when one of the stimuli (S1 and S2, respectively in dark and bright gray contours) wins the race-to-  
 225 threshold to trigger a saccade. Row 3 presents the predicted distributions of saccade landing positions. We  
 226 hypothesized that there could be a homogenous boost of the signals reaching the motor map when the context is  
 227 unfamiliar (a surprise effect). In the control condition (Column 1, Pair Frequency 80%), the pair of stimuli is  
 228 presented only for 80% of the trials while in the test condition (Column 2, Pair Frequency 20%), the pair of  
 229 stimuli is presented only for 20% of the trials. Under the above assumption, we predict that the activity of any  
 230 race loser (S1 or S2, first and second row) should be greater in Pair Frequency 20% than in Pair Frequency  
 231 80%. Thus the bimodal Global Effect would be larger on both stimulus side (third row) when compared to  
 232 control.

233

## 234 4 METHODOLOGY

---

### 235 4.1 PARTICIPANTS

236 Four naïve individuals and the author (25-27 years old; 3 males and 2 females) participated in the  
237 experiment. All had normal visual acuity, were postgraduate at Cardiff University, had given their  
238 written informed consent and received payment for their time. No participants reported drug or  
239 alcohol dependencies or sleeping disorders. Ethical approval was obtained through the local ethics  
240 committee. All but one were naïve to the purpose of the experiment

### 241 4.2 APPARATUS

242 Participants performed the experiment in a quiet dark room. They sat at a distance of 72 cm from a  
243 CRT monitor (ViewSonic P225f) with a 100 Hz refresh rate. Its dimensions were 36.60 cm in width  
244 and 29.30 cm in height for a density of pixels approximately 35 PPCM (pixels per centimeter). The  
245 monitor was covered with a red filter. Eye movements were recorded with an EYELINK 2000 system  
246 (Tower mount system; SR Research Ltd., Canada), an infra-red video-based eye tracker that has a  
247 spatial resolution of  $0.01^\circ$  and a typical average accuracy between  $0.25^\circ$  and  $0.5^\circ$ . It was used at a  
248 time resolution of 1000 Hz while the participant's chin was resting on the headset pad. Only the left  
249 eye was recorded. The experiment was programmed with *pygame*, a python library that provides  
250 graphic and input management, and *pylink*, the official EYELINK library for python. All the analyses  
251 were conducted with *scipy* (McKinney 2010), the scientific package for python (e.g.  
252 [www.python.org](http://www.python.org)), and with *ipython* 2.0 (Perez and Granger 2007). The source code and data are  
253 available on the open science framework ( <https://osf.io/9adbk/> ).

254

### 255 4.3 STIMULI AND PROCEDURE

256 All the trials followed the same template: the participant started by staring at a white fixation cross  
257 of radius  $0.4^\circ$  (luminance:  $4.5 \text{ cd/m}^2$  except when stated otherwise) on a black background at the  
258 center of the screen. After a random interval of 500-1000ms, the fixation cross disappeared and a  
259 target element was presented at an eccentricity of  $13.5^\circ$  (see **Figure 4A** and **B**) while its direction  
260 could have been any one of the 32 directions tested. We tested 8 directions per quadrant (given in  
261 directional angles, see **Figure 4A**): from  $+5.625^\circ$  to  $+45^\circ$  by steps of  $5.625^\circ$  for the top right quadrant;  
262 and reciprocally for the other quadrants (see **Figure 4A**). For a certain percentage of the trials (double

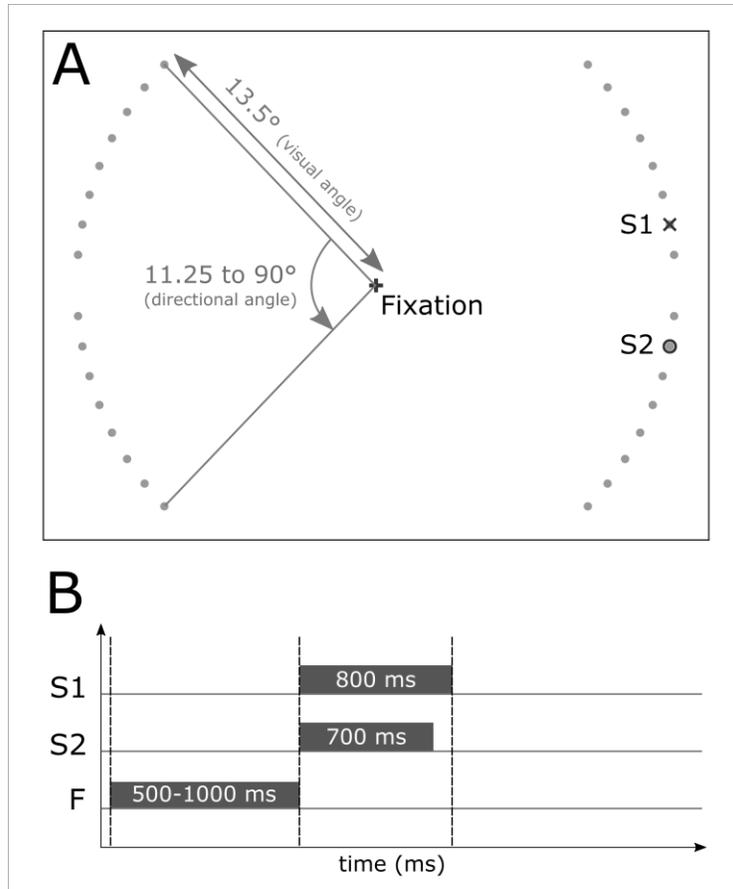
263 stimulus trials), an additional stimulus is simultaneously displayed at the horizontal mirror image of  
264 the target: if the target is presented in the top part of the screen (e.g. at 45°), the additional stimuli  
265 will be displayed symmetrically in the bottom part of the screen (e.g. at -45°). The stimuli remained  
266 present until after the end of the saccades analyzed here. Following this, the screen was cleared and  
267 a new trial began.

268 We tested the effect of the task performed by the participants when a pair of stimuli was presented  
269 (Task-Type). In Free Choice Task conditions (Free Choice), the additional stimulus was identical to  
270 the target but 12.5% brighter. For these conditions, the participants were simply asked to move their  
271 eye to any presented stimulus as quickly and precisely as possible. They did not receive further  
272 instructions for the case of double-stimulus trials. In the Discrimination Task (Discrimination), the  
273 additional stimulus was of a different shape to the target and was also 12.5% brighter. For these  
274 conditions, the participants were instructed to ignore the distractor and to move their eyes to the  
275 target as quickly and precisely as possible. For different blocks, the distractor and the target of  
276 *Discrimination* conditions could either be a circle or a diagonal-cross of 0.8°. The distractor logically  
277 inherited the remaining shape: it was a circle if the target was a diagonal-cross and vice versa.

278 We tested the effect of frequency of occurrence of the pair of stimuli: in High Frequency conditions  
279 (F-80), the additional stimulus was presented 80% of the time, while, in Low Frequency conditions  
280 (F-20), its frequency was set up at 20%.

281 One experimental session would test one of the 4 following combinations: *F-20/Free Choice, F-*  
282 *20/Discrimination, F-80/Free Choice, F-80/Discrimination*. For all the participants, the sessions were  
283 ordered as follows: *F-20/Free Choice, F-20/Discrimination, F-80/Free Choice, F-80/Discrimination, F-*  
284 *80/Discrimination, F-80/Free Choice, F-20/Discrimination, F-20/Free Choice*. While we would usually  
285 counterbalance the order across participants, here we thought it was useful to keep this order since  
286 surprise in F-20 conditions is part of the design rationale and participants were not told whether  
287 there will be double-stimulus trials. The palindrome order within participant was used to minimize  
288 any linear training effects. We also check that our results hold when order effects are taken into  
289 account.

290 The participants were required to undertake 8 sessions of 1600 trials each (8x60min); each session  
291 being separated at least by one night. A break was offered every 200 trials while a break and a  
292 calibration on 13 points were imposed at every 400 trials.



293

294 **Figure 4: Summary of the Paradigm.** **A:** the possible positions of the stimulus on the monitor's display during a  
 295 trial (light gray dots); the eccentricity of the stimuli was always of  $13.5^\circ$  while their directional angles varied  
 296 from  $5.625$  to  $45^\circ$  (by step of  $5.625$ ). The stimulus pair in double-stimulus trials was always symmetrical that one  
 297 stimulus was presented in the upper hemi-field and the other in the lower hemi-field (same eccentricity, opposite  
 298 directional angles). The schematic illustrates a Discrimination Task trial where the S1 (in dark gray) is a  
 299 diagonal-cross and the additional stimulus S2 (in dark gray) is a circle. Note that the color of the background  
 300 and stimuli are not respected in this schematic, and the array of possible stimulus locations (light grey dots) was  
 301 not visible to the participant. **B:** A pair of stimuli – S1 and S2- appeared on the screen simultaneously after the  
 302 offset of the fixation cross F.

303

## 304 4.4 DATA ANALYSIS

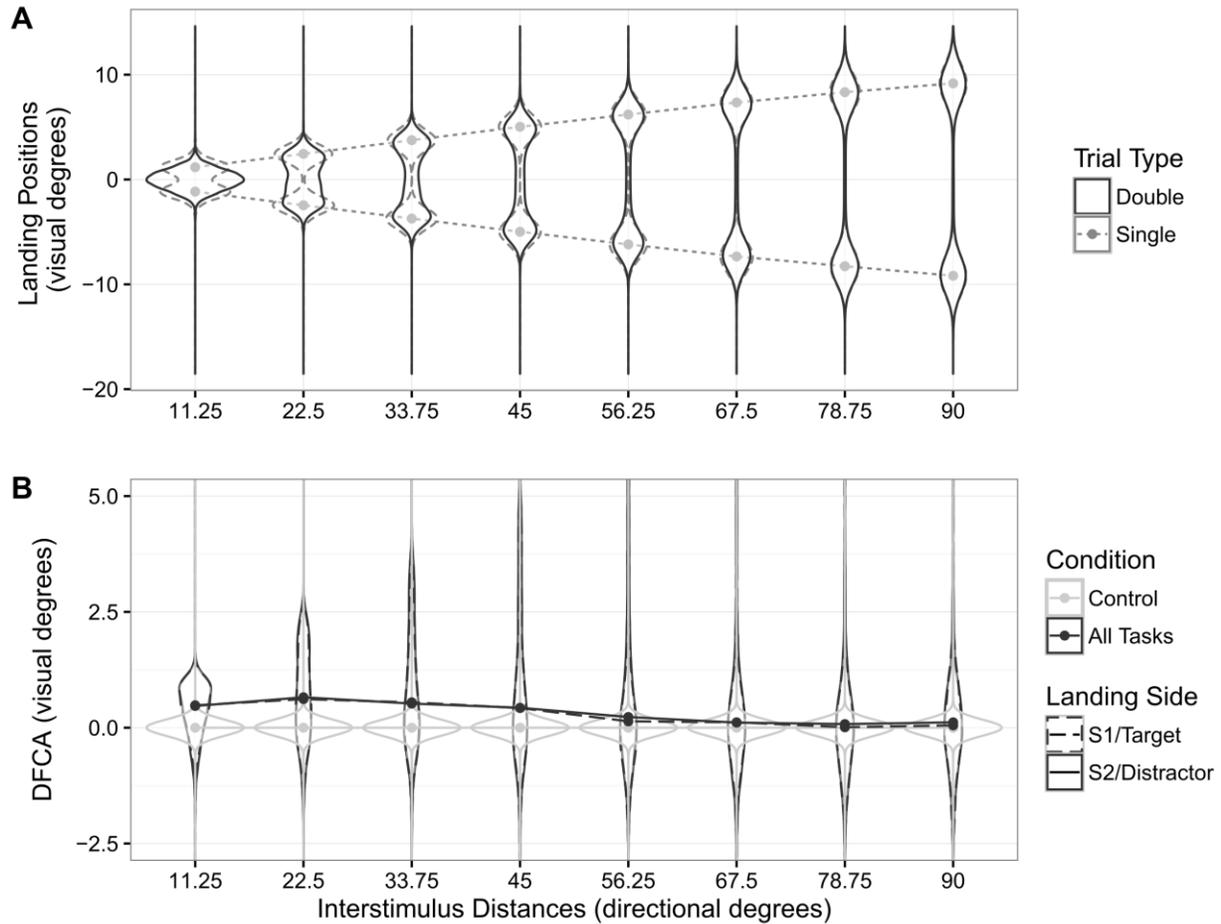
### 305 4.4.1 Saccade Detection and Cleaning

306 Saccade end points were detected as the first data point with a velocity below  $10^\circ.s^{-1}$ , an acceleration  
 307 below  $6000^\circ.s^{-2}$ , and a shift from the previous fixation above  $1.0^\circ$ . Then saccade start points were  
 308 detected as the last data point (backward from the saccade end point) at which the eyes had a velocity  
 309 below  $30^\circ.s^{-1}$ , an acceleration below  $6000^\circ.s^{-2}$ , and a shift from previous fixation below  $0.3^\circ$ . The  
 310 difference in criteria for saccade end and start points were implemented to deal with an artifact that

311 can occur at the end of saccades (see (Nyström et al. 2013), for more information of this post-saccadic  
312 oscillation artifact). Trials were automatically marked as suspect and inspected if: 1) there were  
313 missing values or gaze positions outside the monitor during the saccade, 2) no entire saccade was  
314 detected, 3) the reaction time from target onset was less than 80ms, 4) the saccade duration was  
315 longer than the reaction time, and 5) the position shift from the fixation was less than 7.5°. In  
316 addition, the experimenter could allow some trials that presented a position outside the monitor  
317 display, or reject a trial that presented a blink. After cleaning, the loss rates were 1.7%, 1.5%, 4.5%,  
318 3.4% and 2.2% (given for each of the 5 participants). Note that we included all the saccades made  
319 toward Target and Distractor side in the Discrimination task. We also included all the saccades  
320 toward S1 and S2 in the Free Choice task.

#### 321 **4.4.2 Measure of the Global Effect: Distance From the Closest Attractor**

322 The landing positions correspond to the endpoint positions of the first saccade produced after the  
323 onset of the stimuli. Note that for each of the 8 stimulus distances that we tested, there were 4  
324 possible target positions (one per quadrant); for the analysis, the data were mirrored and combined  
325 across these.



326

327 **Figure 5: Landing Positions and Distance From the Closest Attractor.** We used violin plots to present the  
 328 data distributions – the larger the violin, the denser the data points at that y-position. For instance, **in A**,  
 329 the dark violin for the inter-stimulus distance 11.25 shows a unimodal distribution of landing positions centered on 0  
 330 – that is exactly between the two stimuli. The brighter violin is the control distribution from single-stimulus trials  
 331 with the same locations. The dashed lines are the means of the control modes. While the inter-stimulus distance  
 332 increases, the distribution splits progressively into a bimodal distribution that is eventually indistinguishable  
 333 from control. **In B**, we plot the distance from closest attractor (DFCA), so that the transformation can be  
 334 observed by comparing the top plot and the bottom plot (see section 4.4.2 for further details). The DFCA on each  
 335 side is simply the landing positions in double-stimulus trials centered on the mean of the landing positions in  
 336 single-stimulus trials. The lines with dots represent the means of the distributions. The data are from all the  
 337 participants and all conditions.

338

339 To measure the bimodal GE, we divided the landing positions into two groups one directed towards  
 340 the target, and another directed towards the distractor. For each group, we computed a control  
 341 landing position from the single-stimulus trials. We then examined the deviation of each group from  
 342 their control. The controls were computed across the four screen quadrants (we mirrored the data  
 343 and collapsed them to one quadrant), and are distance specific (e.g. one control per distance),  
 344 participant specific, and block specific (to correct for calibration discrepancies). We named the

345 measure the Distance From the Closest Attractor (DFCA) – the attractors being the control positions.  
346 For the landing position  $i$  and on the  $y$ -axis, this is defined mathematically, by:

$$347 \quad DFCA_i = \min(|C_1 - y_i|, |C_2 - y_i|)$$

348 Where  $C_1$  and  $C_2$  are the control position. **Figure 5** shows the DFCA for saccades directed toward the  
349 target. Note that another major difference with the usual measure of the GE is that we get one  
350 measure per trial, which increases the statistical power.

#### 351 **4.4.3 Statistical analysis**

352 To test statistically the difference in DFCA across conditions and distances, the saccades of all the  
353 participants were gathered (as in Van der Stigchel & Nijboer, 2013). This led to an average of 389  
354 trials for each distance in each condition for the conditions *Free Choice / F-20* and *Discrimination / F-*  
355 *20* and an average of 1,543 trials for conditions *Free Choice / F-80* and *Discrimination / F-80*. The  
356 proportion of landing positions between the two stimuli was reasonably balanced in all conditions  
357 and participants. Given that the distributions of DFCA are clearly non-normal and have different  
358 shapes across distances, we used the non-parametric independent 2-group Mann-Whitney U-test to  
359 test for mean differences (the `wilcox.test(x, y, paired=FALSE)` in R). In order to focus on  
360 differences within participants, and because the U-test does not apply this by itself, we applied a  
361 within-subject correction (Cousineau 2005) by centering the data of each participant on the same  
362 mean.

363 Using the DFCA, we ran one U-test for each of the eight stimuli distances testing for an effect of *Task-*  
364 *Type (Discrimination against FreeChoice)*. The same procedure was repeated to test the effect of *Pair-*  
365 *Frequency* across stimuli distances (level *F-20* against level *F-80*). The p-values for a set of tests were  
366 corrected according to Hommel's correction, which has been recommended for adjusting mildly  
367 correlated p-values (Blakesley et al. 2009). We report, in Figure 7, the Hodges-Lehmann estimator  
368 (HLΔ) – i.e., the median of pairwise differences in bimodal GE between two conditions. This can be  
369 interpreted as the GE modulation between the two tested conditions. A complete report of the U-test  
370 statistic can be found on the OSF repository.

## 371 5 RESULTS: DISTANCE FROM CLOSEST ATTRACTOR

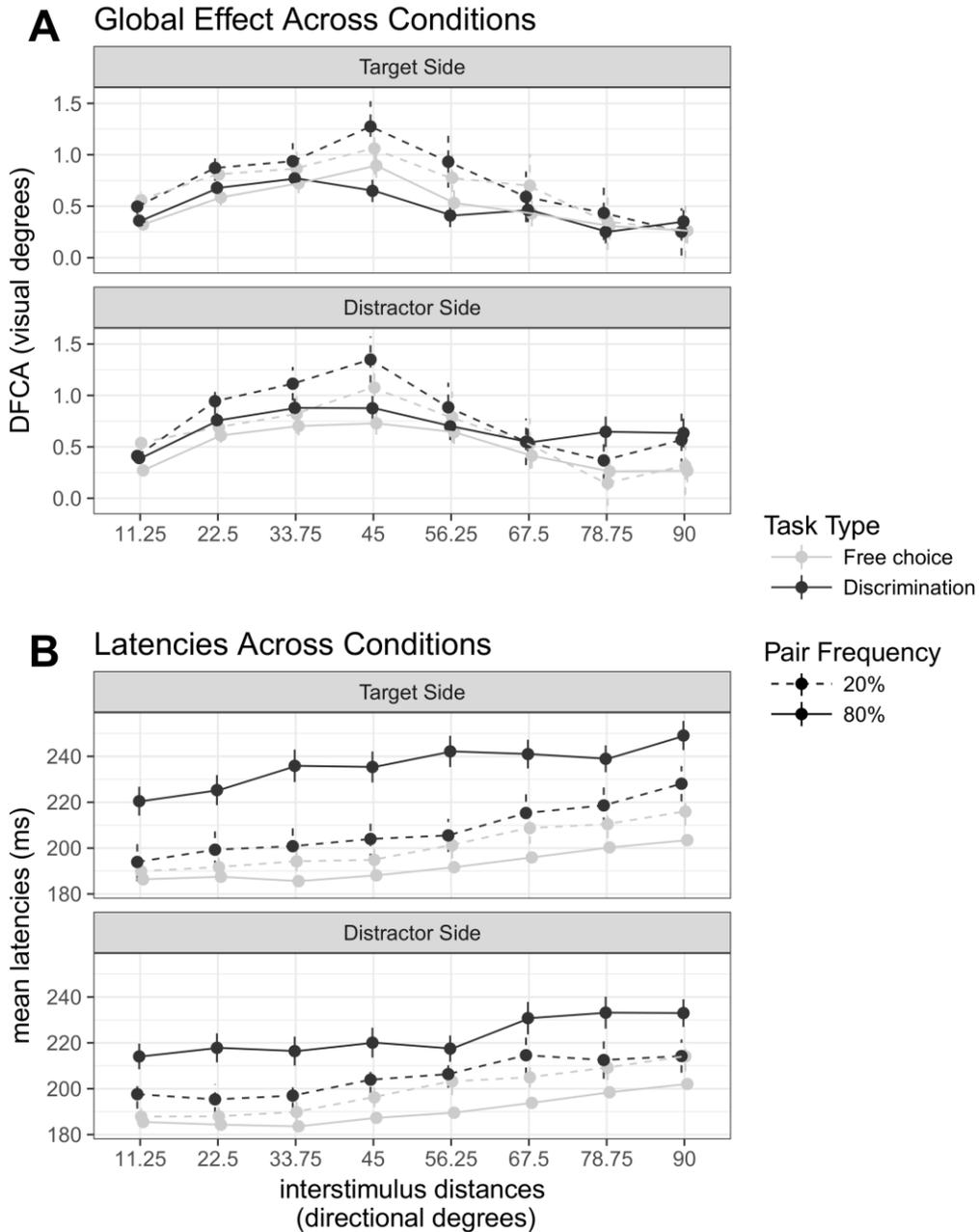
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### 372 5.1 OVERVIEW OF THE BIMODAL GE

373 Observation of **Figure 6A** reveals a clear bimodal GE effect, and that the DFCA initially increases and  
374 then decreases with stimulus distance (one-way ANOVA,  $F(7, 28)=2.9$ ,  $p = .02$ ,  $\eta_g^2=.42$ ), which is how  
375 the GE was expected to fluctuate. **Figure 6B** reveals that latencies increase with stimulus distance in  
376 all conditions (one-way ANOVA,  $F(7,28)=9.9$ ,  $p<.001$ ,  $\eta_g^2=.712$ ); this could, at least partially, explain  
377 the aforementioned decrease of bimodal GE. Note that this tendency is also present in FreeChoice,  
378 where there is no discrimination to perform. Thus, lesser Global Effect with longer latency could be  
379 interpreted as a stronger commitment to one stimulus with time.

380 Figure 7 shows landing positions of a representative participant both in visual and SC space. The  
381 landing positions are distributed along a straight line (slightly curved inward) in visual space and  
382 along a C-curve when projected in an approximation of the human SC space (based on the monkey  
383 data in Robinson 1972; according to Ottes et al. 1986 's equations). As discussed in Introduction, this  
384 pattern is what we would expect from a saccadic vector averaging mechanism; and it echoes back to  
385 the pattern obtained when applying simultaneous, weighted supra-threshold micro-stimulations to  
386 the SC (Katnani and Gandhi 2011; Katnani et al. 2012).

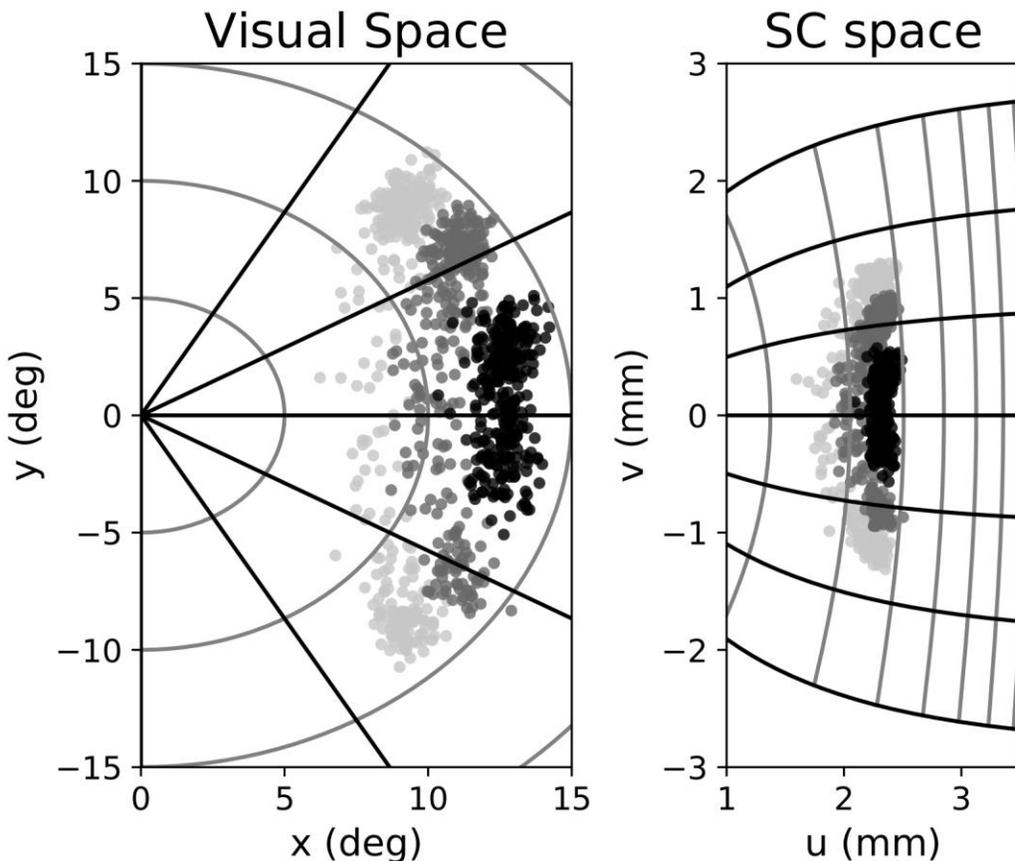
387



388

389 **Figure 6: Overview of the Distance From the Closest Attractor (DFCA) and Latencies over stimuli**  
 390 **distances and between conditions.** The figure shows the mean of the distributions with the parametric 95%  
 391 confidence intervals; the top part displays the curves for the DFCA on the target side, and the bottom part  
 392 displays the curves for the DFCA on the distractor side.

393



394

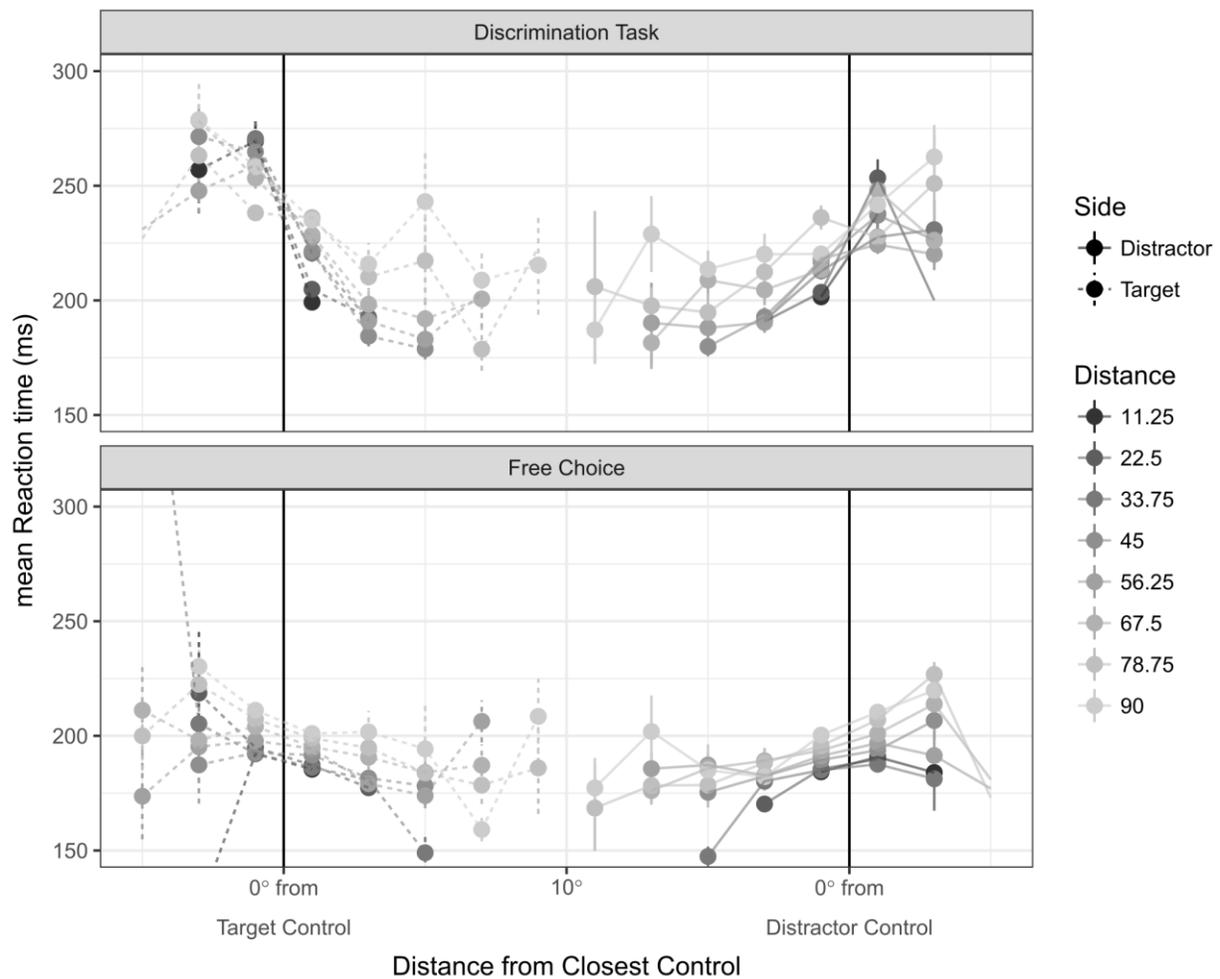
395 **Figure 7: Distribution of Landing Positions in visual space and Superior Colliculus (SC) space from a**  
 396 **representative participant.** Distributions are shown for inter-stimulus distances  $90^\circ$  (light grey dots),  $67.5^\circ$   
 397 (medium gray dots) and  $33.75^\circ$  (dark gray dots) in F80/Discrimination Task. The distributions followed an  
 398 inwards C-curve on the SC space; this was a consistent pattern across conditions and participants (the figures for  
 399 all participants are accessible on the OSF repository). The landing position were projected to an approximation  
 400 of the human SC space; using Ottes et al.(1986)'s equations and its original set of parameters that estimates the  
 401 electrical stimulation data from Robinson (1972) on monkey.

402

403 As noted in introduction, it is important to establish that the bimodal GE is modulated in size in a  
 404 systematic way consistent with representing the losing activity in an incomplete decision process.  
 405 We expect that saccades landing in between the two stimuli would have the shorter latencies, driven  
 406 by early nonspecific visual transients that are equivalent for both stimuli. Smaller deviations and  
 407 accurate saccades (to either the target or distractor) would be associated with longer latency when  
 408 the decision process has progressed towards a unique winner (i.e. the losing activity has diminished).  
 409 Figure 10 shows that these predictions are confirmed in our data, consistently for every condition  
 410 and every distance between the stimuli. Note also that saccades with larger GE (i.e. around the

411 midpoint of the two stimuli) are more similar in latency across all conditions than saccades with  
 412 smaller GE, consistent with our understanding of non-specific early visual transients followed by  
 413 slower signals that are more task-modulated.

414  
 415  
 416  
 417  
 418



419

420 **Figure 8: Reaction times in relation to the bimodal GE (or Distance from the Closest Attractor).** The mean  
 421 reaction times are plotted for each 2 degree bins of the Distance from the Closest Attractor distribution. The  
 422 DFCA was introduced in Figure 5 and is our measure of the bimodal GE.

423

424

## 425 **5.2 ASYMMETRIC EFFECT OF TASK-TYPE ON BIMODAL GE**

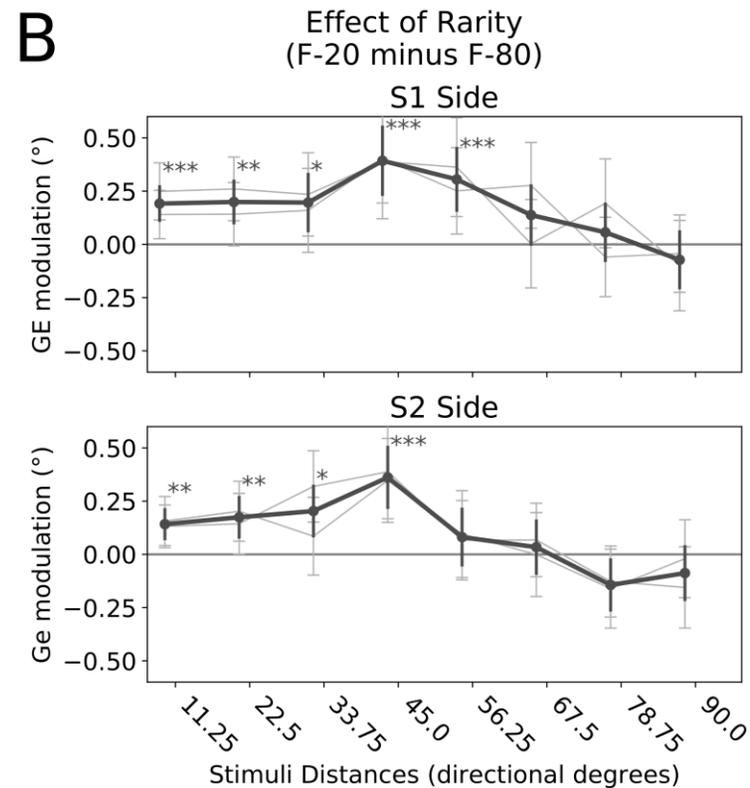
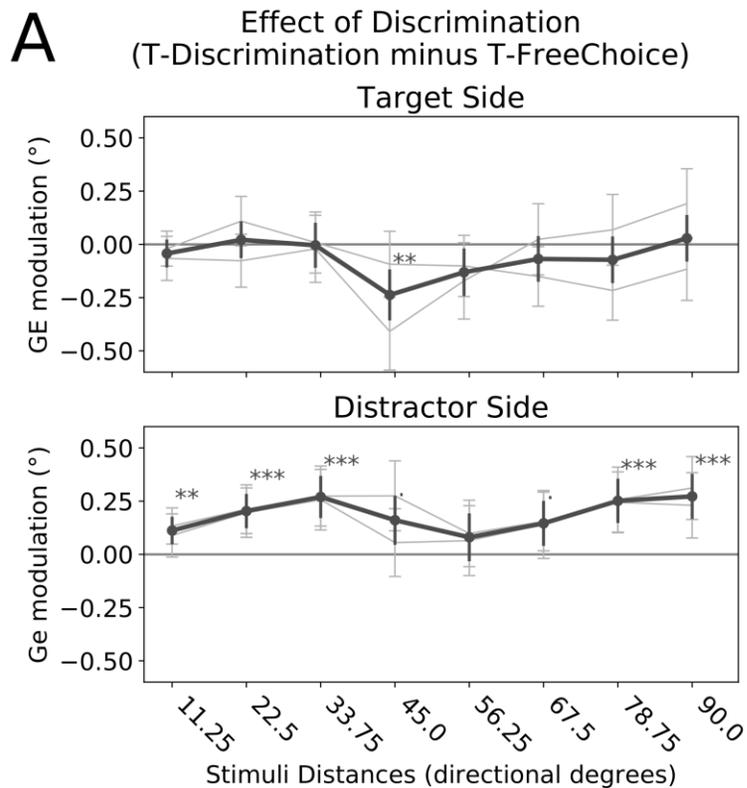
426 **Figure 9A** corresponds to the effect of *Task-Type* on GE, which is the difference between the dark  
427 and light gray curves in **Figure 6A**. The U-tests revealed a significant effect on the DFCA only at one  
428 distance (45°) on the target side, but a consistently significant effect for all distances but one (56.25°)  
429 on the distractor side. Furthermore, the effect observed at 45° on the target side is a decrease in GE  
430 (shift toward the target) whereas the effect on the distractor side is a consistent increase in GE (shift  
431 toward the center) (**Figure 9A**, the exact statistical values are reported in the appendix). In  
432 particular, that increase of GE on the distractor side is rather regular over stimulus distances if we  
433 ignore the decrease at 56.25°; certainly, it does not show a monotonic decrease with distance. In  
434 summary, we observe an asymmetric increase in the GE when the participant is asked to aim towards  
435 a target and avoid a distractor (Discrimination) – the clearest effect is that the saccades directed to  
436 the distractor tend to be shifted toward the center (towards the target). That result when interpreted  
437 along with the **Figure 2** suggests that the discrimination mechanism is applying a boost on the target  
438 side and little or no inhibition on the distractor side: when the target loses the race, its activity at the  
439 moment the saccade was executed was higher in the discrimination task than in the free choice task,  
440 but when the distractor loses the race there is not much detectable difference in its activity level  
441 between tasks.

442 These GE modulations are not likely to be explained by the latencies. **Figure 10A** shows the effect of  
443 Task-Type on latencies, which is the difference between the dark and light gray curves in **Figure 6B**.  
444 The U-tests revealed that latencies are greater in the Discrimination task than in the Free Choice task  
445 on both stimulus sides (Target and Distractor). The effect size is slightly greater on Target side (mean  
446 HLA ~ 20 ms) than Distractor side (mean HLA ~ 13ms; Welch Two Sample  $t(9.12) = -4.55, p = .001$ ).  
447 Although the GE is known to negatively correlate with latencies, that difference of 7 ms is not likely  
448 to explain the asymmetry in GE observed in **Figure 9A**. In comparison, the work of Heeman et al.  
449 (2014) suggests that a difference of ~120ms is needed to observe a total suppression of GE. Finally,  
450 **Figure 6B**, suggests an interaction effect of Frequency with Task Type on latencies (confirmed  
451 below); the effect of Discrimination (over FreeChoice) is less in F20 (compare the dashed curves)  
452 than in F80 (compared the solid curves). Such an interaction effect does not seem to be present for  
453 the GE (**Figure 6A**) and could not explain the GE modulation observed in **Figure 9A**.

### 454 **5.3 SYMMETRIC EFFECT OF PAIR-FREQUENCY ON BIMODAL GE**

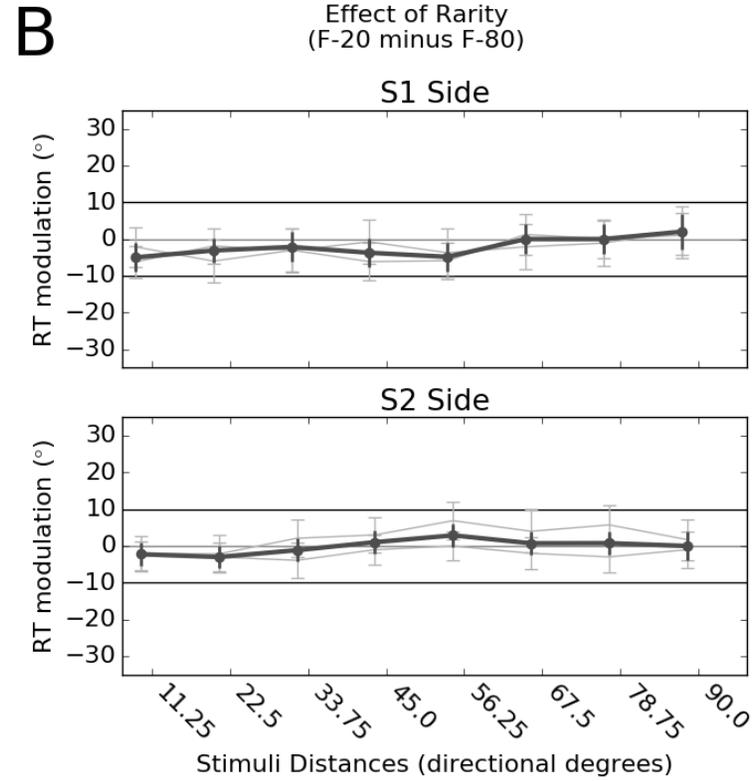
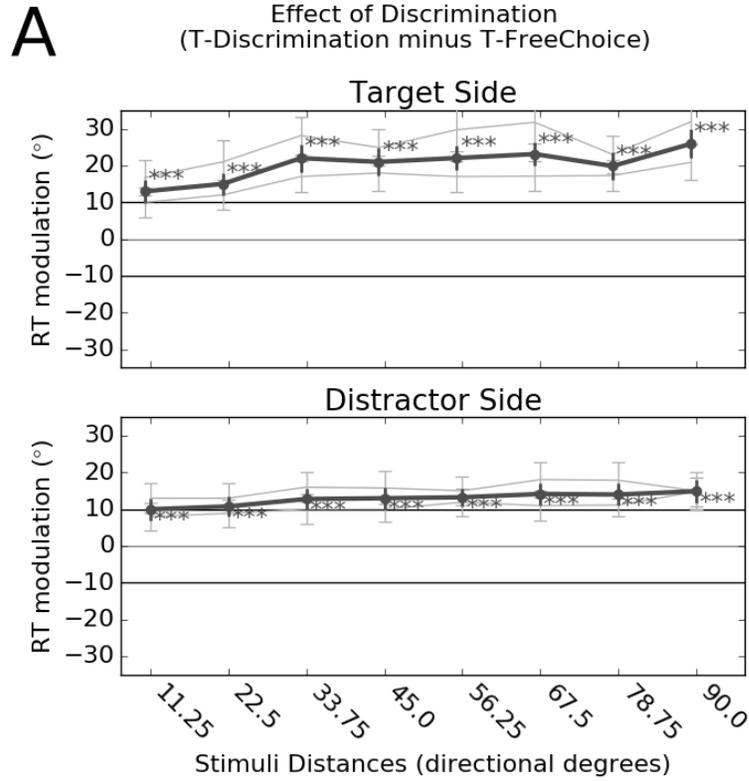
455 **Figure 9B** shows the effect of *Pair-Frequency* on GE, which is the difference between the dashed and  
456 solid curves in **Figure 6**. The U-tests yielded significant effects of *Pair-Frequency* both on S1 side and  
457 S2 side (we are now ignoring whether they were target or distractor). In particular, **Figure 9B**  
458 suggests a symmetric increase of the GE when double-stimulus trials are rare (F-20), which tends to  
459 increase progressively with the inter-stimulus distance up to distance 45°, upon which it decreases.  
460 The only possible asymmetry is that the effect of F-20 on the S2 side tends to decrease more rapidly  
461 with the inter-stimulus distance in comparison with the S1 side. This small asymmetry could be  
462 attributed to the slight difference in luminance between stimulus S1 and S2. In summary, this pattern  
463 of results, when interpreted in light of the **Figure 3**, suggests that the effect of rarity is to generally  
464 increase stimulus-related activity on the motor map (i.e. to both stimulus sides).

465 Again, these GE modulations are not likely to be explained by differences in latencies. **Figure 10B**  
466 shows the effect of Frequency on latencies, which is the difference between the dashed and solid  
467 curves in **Figure 6B**. The U-tests revealed that there is no obvious latency modulation between F20  
468 and F80 conditions, so that it cannot explain the GE modulations. This lack of effect is explained by  
469 the interaction of Frequency with Task Type on latencies that we noted above (**Figure 6B**). F20  
470 (when compared to F80) increases the latencies in the Free Choice task (see the difference between  
471 the light gray curves) while decreasing the latencies in the Discrimination task (see the difference  
472 between the black curves). The sum of these positive and negative effects leads to a null effect.



473

474 **Figure 9: Summary of the Mann-Whitney U-tests on Global Effect.** Each plot shows the difference in DFCA between the two conditions, which we name  
 475 the GE modulation: a positive number means that there is a larger GE (greater deviation towards the center) in Discrimination than in Free Choice  
 476 conditions (in **subplot A**) or a larger GE in F-20 than in F-80 conditions (in **subplot B**). The modulation in GE – thick dark curves – is estimated with the  
 477 Hodges–Lehmann estimators (HLΔ) with 95% confidence intervals. The stars represent the level of significance (\*\*\*  $p < .001$ ; \*\*  $p < .01$ ; \*  $p < .05$ ; .  $p < .1$ ). Finally,  
 478 the thin gray curves display separately the GE modulation in the first and second block of each conditions (see method). **A:** We ignored the factor Pair-  
 479 Frequency, mixing the conditions F-20 and F-80. **B:** We ignored the factor Task-Type, mixing the conditions Free Choice and Discrimination. Note that we  
 480 refer to S1 and S2 as the two stimuli presented simultaneously; S2 corresponds to the slightly brighter one in Free Choice conditions and to the distractor in  
 481 Discrimination conditions.



482

483 **Figure 10: Summary of the Mann-Whitney U-tests on Latencies.** Each plot shows the difference in Latency between the two conditions, which we named  
 484 RT modulation. The organization is the same as in Figure 9.

485

486 In order to test whether there is indeed an interaction of Frequency and Task Type on latencies, we  
 487 ran a Bayesian Top-down analysis, using R's BayesFactor package (Raftery 1995; Rouder and Morey  
 488 2012), where we compared a full model (explicitly given in the caption of Table 1) to models that  
 489 omit one main effect or interaction from that full. From this analysis, we can see that there is indeed  
 490 an interaction effect between Task Type and Frequency on reaction times (row 4 of Table 1, BF >  
 491 1000). Note that we could not run this test on bimodal GE because its distribution varies across  
 492 distances.

493 Table 1. Bayesian Top-down Analysis on Reaction times.

	Omitted variable	BF or 1/BF	Polarity	Interpretation T
[1]	Frequency:Side:TaskType	1.8 ±4.9%	none	weak
[2]	Frequency:Side	8.1 ±6.3%	against	positive
[3]	Side:TaskType	>1000 ±10%	in favor	very strong
[4]	Frequency:TaskType	>1000 ±92 %	in favor	very strong
[5]	Participant	>1000 ±5.9%	in favor	very strong
[6]	Distance	>1000 ±12%	in favor	very strong
[7]	Side	>1000 ±12%	in favor	very strong
[8]	Frequency	>1000 ±10%	in favor	very strong
[9]	TaskType	>1000 ±11%	in favor	very strong

494 *Note. BF stands for Bayes Factor. We inverted (1/BF) the BFs less than 1 for easier reading. We add a*  
 495 *Polarity column that tells if the evidence quantified by the BF is against or in favor of an effect of the*  
 496 *omitted variable (e.g. Side:TaskType). The interpretation tags give a qualitative scale to that evidence,*  
 497 *as in Raftery (1995). The symbol ':' denotes an interaction. For instance, the third row reads: there is*  
 498 *very strong evidence in favor of an interaction effect between Side and TaskType. The BFs are given*  
 499 *against the full model:  $RT \sim \text{TaskType} * \text{Frequency} * \text{Side} + \text{Distance} + \text{Participant}$  with Participant as a*  
 500 *random variable (to account for the within participant design). Side refers to the side*  
 501 *(Target/Distractor or S1/S2) on which are the landing positions.*

502

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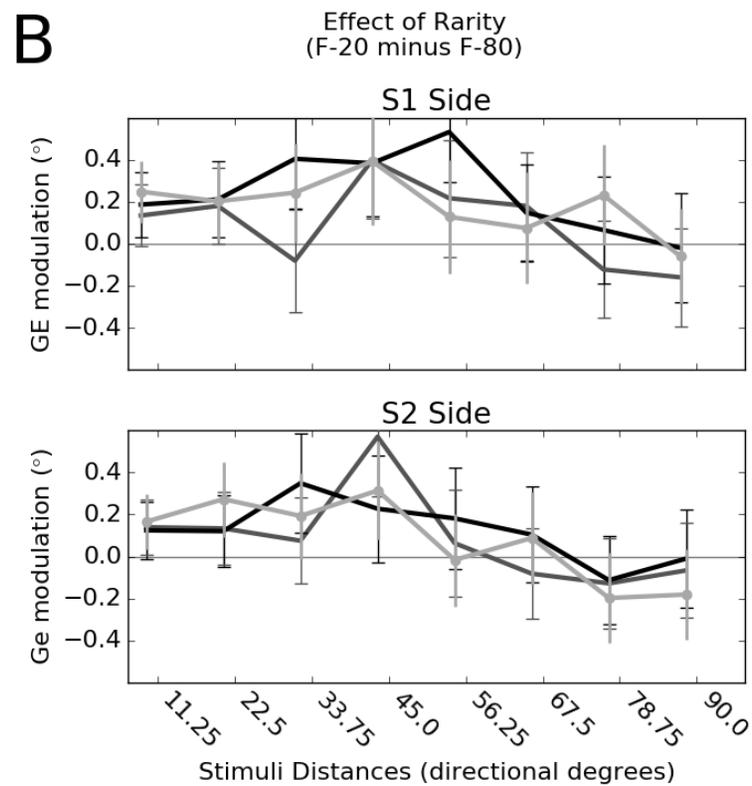
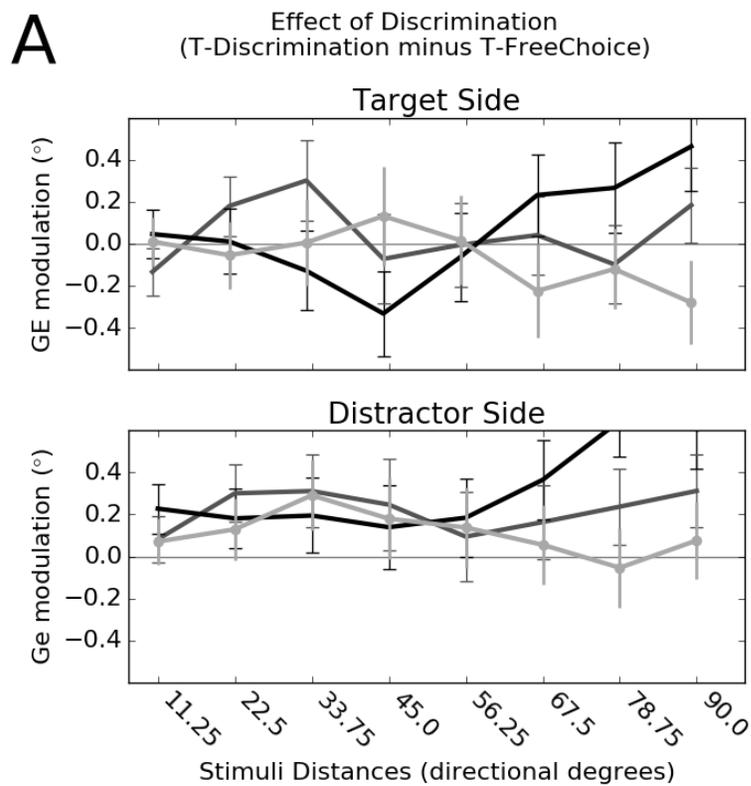
505

#### 506 5.4 INTRA-INDIVIDUAL LATENCIES AND BIMODAL GE

507 Finally, although we checked whether the change in mean latency across conditions could explain the  
508 change in bimodal GE, the intra-participant latency distributions could still explain part of our results.  
509 For instance, it can be argued that the lack of effect on the GE modulation on Target side (**Figure 9**)  
510 originates from a mixture of a positive GE modulation for early saccades and a negative GE  
511 modulation for late saccades. This explanation would echo the early deviation toward and late  
512 deviation away found in saccade curvature (McSorley 2006). **Figure 11** shows the same data as in  
513 **Figure 9**, except that we divided the saccade distribution into early, middle and late saccades (see  
514 the light gray, dark gray and black curves respectively). We found no consistent effect of latency  
515 groups on the bimodal GE across distances on the Target side (Figure 9A) so that the lack of target-  
516 side effect observed in Figure 7A cannot be accounted by an interaction with latencies. On the  
517 Distractor side, a more consistent pattern is observed: no effect of latencies for distances below 56.25  
518 after which early saccades lead to small or no GE modulation while late saccades lead to large and  
519 positive GE modulation (this ordering may be present for these distances for the target side as well).  
520 We will come back to this interesting pattern in the discussion. Finally, concerning the effect of rarity,  
521 it seems that there is no obvious effect of the latency groups on the GE modulation.

522 Recall that we used a particular palindromic ordering for the different conditions. A Wilcoxon rank  
523 sum test on the DFCA between the first block and the second block of *F-20/Free Choice* reports a  
524 significant difference ( $W= 12E+7$ ,  $p=0.002$ ) with a small effect size ( $-0.04^\circ$ ) compared to the effects  
525 observed in **Figure 9** (from  $0.2^\circ$  to  $0.4^\circ$ ). Thus, it appears that any extra surprise effect in the first  
526 block was small or did not last long enough within the block to produce a large overall effect. Finally,  
527 it is important to note that our results are robust despite order effects. Figure 7 shows no great  
528 change in GE modulation when taking into account either the first or the second block of each  
529 condition (thin gray curves).

530



531

532 **Figure 11: Effect of Latency Quantile on GE modulation.** The organization is the same as in **Figure 9** except that we split the GE modulation into three  
533 groups: early, middle, and late latency saccades, respectively in light gray, dark gray and black.

534

535

## 536 6 DISCUSSION

---

537 In the present study, we demonstrated that, when using a pair of remote stimuli, a bimodal Global  
538 Effect (GE) occurs – i.e., both distribution modes deviated toward the other stimulus. This confirms  
539 previous reports where such an effect was shown or appeared present (Arai et al. 2004; Van der  
540 Stigchel et al. 2007, 2011). Moreover, 1) this deviation appears to occur on a nearly- straight line in  
541 visual space, and a strong curve in SC space – rather than a straight line in SC space and an outward  
542 curve (a circumference around fixation) in visual space; 2) larger deviations are associated with  
543 shorter latency. These patterns are consistent with the model architecture illustrated in Figure 1D,  
544 whereby a strong region of activity triggers a saccade while the decision process is not fully complete.  
545 Other activity remains on the map and contributes towards saccade vector programming  
546 downstream of the SC.

547 From this perspective, the deviation of the landing position from the race winner –that is the closest  
548 stimulus - gives an estimate of the activity of the race loser. It can then be used to assess endogenous  
549 enhancements or inhibition that the traditional GE could not distinguish. Furthermore, it can assess  
550 these signals over a wider range of interstimulus distances. We found that Task-Type and Pair-  
551 Frequency draw two clearly distinguishable patterns in terms of modulating the GE. We discuss  
552 further below the interpretation of our results, in terms of their spatial profile, underlying  
553 mechanisms, and their link with the previous literature.

554

### 555 6.1 EFFECT OF DISTANCE ON THE BIMODAL GLOBAL EFFECT

556 According to Walker et al. (1997) and Van der Stigchel and Nijboer (2013), the genuine (unimodal)  
557 GE is expected to decrease with stimulus distances. We also found this relationship in the bimodal  
558 GE (see **Figure 6A**). This may be partly explained by RT increasing with distances. However, the  
559 range of 20ms may be too small to explain the total disappearance of GE (~120ms needed in Heeman  
560 et al. 2014). In our frame of explanation, this decrease in GE with stimulus distance may also be  
561 caused either by: 1) a hypothetical stronger mutual inhibition between the two stimuli whilst their  
562 distance increases – decreasing the activity of the loser or 2) a spatially localized release of the  
563 inhibition exerted by substantia nigra pars reticulata (SNr) on the SC – remote losers would benefit  
564 less from disinhibition centered on target location (Hikosaka and Wurtz 1983; Handel and Glimcher  
565 1999; Basso and Wurtz 2002). Note that 1) would contradict the relatively flat curve of inhibition

566 reported in previous modelling and neurophysiological work (Arai et al. 1994; Trappenberg et al.  
567 2001).

568

## 569 **6.2 MODULATION OF THE GLOBAL EFFECT BY DISCRIMINATION SIGNAL**

570 It is often assumed in discrimination tasks that top-down mechanisms facilitate the target-related  
571 activity and/or inhibit the distractor-related activity (Schall and Hanes 1993; Schall et al. 1995;  
572 Wardak et al. 2002; Ipata et al. 2006; Thomas and Paré 2007). Our work shows that the  
573 discrimination signal consistently increases the bimodal GE on the distractor side and had no  
574 consistent effect on the GE on the Target side. If we recall the predictions of **Figure 2**, which use the  
575 model described in **Figure 1D**, the increase of GE on the distractor side means that that the activity  
576 of competition loser – the target – was stronger in the Discrimination Task than in Free Choice (right-  
577 hand column in Figure 2). In other words, our results suggest that the discrimination signal is  
578 facilitating/boosting the target rather than inhibiting the distractor. This result is in line with  
579 neurophysiological data reporting more post-stimulus activity in FEF and SC on the target side during  
580 visual search (McPeck and Keller 2002; Fecteau and Munoz 2006) and no obvious inhibition on the  
581 distractor side in the SC before the saccadic burst (White et al. 2012).

582 However, this conclusion may seem to be in opposition with some previous work. Although it has  
583 been shown that saccade planning enhances processing at target location (Kowler et al. 1995; Deubel  
584 2008), it was also shown that saccade execution suppresses processing at non-target locations (Khan  
585 et al. 2015). Similarly, the Basal Ganglia appear to enhance target location and inhibit distractor  
586 locations (Van Schouwenburg et al. 2013). Finally, it was suggested that local inhibition of the  
587 distractor location could explain saccadic curvature away from a distractor (Tipper et al. 2001;  
588 McSorley et al. 2004). Thus, it seems that further implementation of our paradigm could explore  
589 whether the appearance of inhibition on the distractor can be systematically controlled.

590 The effect of discrimination did not decrease with stimulus distances. This suggests that its  
591 mechanism is not interacting directly with the GE mechanism itself – which does decline with  
592 distance. If that decline is caused by mutual inhibition or the SNr's influence on the SC (hypothesis 1  
593 and 2) discussed above), then the goal-directed boost seems simply additive with those mechanisms.  
594 It is known that the FEF is involved in target discrimination (Schall and Hanes 1993) and has direct  
595 projections to the brainstem saccade burst generator (although their functional role has been  
596 questioned, Hanes and Wurtz 2001), bypassing the SC to control saccades (Schiller et al. 1980;

597 Schiller and Sandell 1983; Schiller and Chou 1998). In the eventuality that the boost to the target is  
598 provided by the FEF, it follows that at least part of this enhancing effect is not altered by the mutual  
599 inhibition and/or the SNr's action in the SC.

600

### 601 **6.3 MODULATION OF THE GLOBAL EFFECT BY FREQUENCY**

602 Previous studies have shown that the probability of a stimulus appearing at a *specific location* can  
603 influence the GE (He and Kowler 1989). Location probability is thought to increase the strength of  
604 the preparatory signal in the SC (Basso and Wurtz 1998; Dorris and Munoz 1998), possibly from the  
605 FEF (Liu et al. 2011), and therefore to decrease the reaction time. Our work goes further and suggests  
606 that probability of occurrence, which, unlike location probabilities, has no spatial dimension, can also  
607 influence the GE. According to our results, the rarity of occurrence of a pair of stimuli increases the  
608 bimodal GE symmetrically, as predicted in Figure 3, and this effect could not be explained by a change  
609 in reaction times. Thus, probability of occurrence tends to enhance the activity related to rare stimuli  
610 configurations and has the opposite effect of the location probability, which enhances the activity of  
611 common locations.

612 It can also be observed that the effect of rarity on GE decreases with stimulus distance, just as the GE  
613 itself decreases with stimulus distance. In other words, rarity is modulating – rather than being  
614 additive with – the underlying GE itself. There are at least two possible ways this could occur: 1) an  
615 increase of the responsiveness of the neurons on the motor map; 2) a decrease of lateral inhibition  
616 on the motor map. The former would modify the gain function of the neurons (i.e. increasing function,  
617 typically sigmoid, linking input current to firing rate) – varying its x offset (gating) and/or slope.

618 Interestingly, the norepinephrine system has been suggested to modify the gain function of neurons  
619 in diffuse parts of the brain involved in decision making through coarse projections (Hurley et al.  
620 2004; Aston-Jones and Cohen 2005). Several studies have suggested that the norepinephrine system  
621 responds to the relevance, novelty, and rarity of stimuli (Alexinsky et al. 1990; Privitera et al. 2010;  
622 Preuschhoff et al. 2011) with more or less habituation effect (Aston-Jones et al. 1994; Vankov et al.  
623 1995). Direct projections of the Locus Coeruleus to the SC have been found (Edwards et al. 1979;  
624 Mooney et al. 1990; Arce et al. 1994) while high and stable concentration of norepinephrine  
625 decreased the spontaneous and/or stimulus-evoked responses in SC (Mooney et al. 1990; Tan et al.  
626 1999; Zhang et al. 1999). Taken together, these findings would encourage investigations into whether  
627 the norepinephrine system could be the mechanism behind the effect of rarity on the strength of the

628 GE. If this is indeed the case, it would open a new avenue of experimental work to test the effect of  
629 the norepinephrine on decision making.

630 Regarding the latencies for our rarity manipulation, we believe there are three interacting factors  
631 acting in different directions: the rarity boost discussed above; caution; spatial probability. In **Figure**  
632 **6B**, in the Discrimination Task condition, the reaction times are smaller in F20 than in F80 while in  
633 the Free Choice condition, reaction times are smaller in F80 than in F20. Concerning the  
634 Discrimination task, an explanation is that frequent discrimination trials (i.e. F80) raises caution,  
635 which leads to slower reaction times. In that case, rare discrimination trials (see black dashed curve)  
636 would lead to lower caution and to similar reaction times as rare free choice (gray dashed curve) –  
637 which is what we observe. Concerning the Free Choice condition, we can consider the opposite effect  
638 of spatial probability: in F80, there is a rate of 1.8 stimuli per trial appearing on the 13.5° eccentricity  
639 ring, while in F20, this rate drops to 1.2. The higher rate leads to a higher spatial probability, which  
640 leads to faster reaction time in F80 as we observed. To conclude, our results suggest that once other  
641 factors are brought into play, what increases the bimodal GE does not necessarily decrease the  
642 reaction times, and vice-versa.

643 In the literature, it has been shown that high probability of occurrence of the target in a go/no-go  
644 paradigm increases the proportion of express saccade (Jüttner and Wolf 1992) while the high  
645 probability of a distractor being present seems to decrease the reaction time on trials in which it is  
646 indeed present (Goldstein and Beck 2013). However, these paradigms may not be testing the same  
647 mechanisms as ours. In Jüttner and Wolf (1992), the saccadic system likely learns to inhibit the go-  
648 signal when the go-trials are rare while our paradigm only has go-trials. In Goldstein and Beck  
649 (2013), it is possible that, because the distractor is informative of the future target timing and  
650 position, it acts as a warning cue.

#### 651 **6.4 CONCLUSION:**

652 The present work has generated a novel way to assess decision processes and signals occurring in an  
653 action selection map such as the SC. In particular, we have examined a different aspect of the Global  
654 Effect which we have termed the bimodal Global Effect (GE). Unlike the traditionally defined Global  
655 Effect (Walker et al. 1997), the bimodal GE can be observed for distant stimuli and for bimodal  
656 distributions. We see it as a tool to measure the modulations that occur on the side of the stimulus  
657 that loses the race to trigger a saccade. Using this framework allowed us to assess in more depth the

658 effect of frequency of choice and of active discrimination on the action selection map. We believe that  
 659 this framework opens a new avenue to explore decision making in general.

## 660 7 APPENDICES

661 [The following tables are given for the reviewers, but they may not be included in the final version.  
 662 They can be found on the open science framework webpage.]

### 663 7.1 TABLES

664 The condition effects (difference between conditions) are reported with the Hodges–Lehmann  
 665 estimator (HLΔ). It is the median of all possible differences between the N measures in one condition  
 666 and the M measures in another condition (N x M combinations).

667 A non-parametric 0.95 confidence interval for HLΔ accompanies these estimates. Finally, the  
 668 Common Language Effect Size (CLES) (McGraw and Wong 1992; Vargha and Delaney 2000) from the  
 669 R package *orddom* is reported. Indeed, the CLES simply estimates the probability that a DFCA  
 670 randomly picked from one distribution is higher than a DFCA randomly picked from another  
 671 distribution – also known as the Probability of Superiority. Generally speaking, a CLES of 0% (or  
 672 100%) would mean that the first distribution is lower (or higher) and does not overlap with the  
 673 second distribution. When the CLES is at 50% the medians of both distributions are aligned.

674

675 *Table 1: Target Side U-tests over distances for a distractor type effect (Free Choice against Discrimination):*

Distance	U-stat		p-value	n.Td	n.Ts	CLES	HLΔ	95% CI
11.25	433851		1.00E+00	981	915	51.67%	-0.040	-0.102 0.022
22.5	460714		1.00E+00	997	909	49.16%	0.028	-0.059 0.115
33.75	458158		1.00E+00	983	930	49.88%	0.005	-0.101 0.110
45	412946	**	2.78E-03	998	914	54.73%	-0.219	-0.338 -0.099
56.25	432647		2.55E-01	1063	863	52.84%	-0.119	-0.230 -0.011
67.5	479230		1.00E+00	1065	925	51.35%	-0.056	-0.161 0.049
78.75	430544		1.00E+00	1035	858	51.52%	-0.062	-0.168 0.045
90	451448		1.00E+00	1007	881	49.11%	0.037	-0.070 0.143

676 *Note. Refer to Table 2 note.*

677 *Table 2: Distractor Side, U-tests over distances for a distractor type effect (Free Choice against Discrimination):*

Distance	U-stat		p-value	n.F8	n.F2	CLES	HLΔ	95% CI
11.25	452304	**	5.10E-03	970	1023	54.42%	-0.118	-0.185 -0.050

22.5	423556	***	5.45E-06	950	1024	56.46%	-0.205	-0.285	-0.125
33.75	413434	***	3.81E-07	948	1017	57.12%	-0.275	-0.373	-0.177
45	451307	*	3.88E-02	953	1022	53.66%	-0.166	-0.282	-0.051
56.25	442758		8.91E-01	877	1054	52.10%	-0.091	-0.204	0.021
67.5	397084	*	3.35E-02	869	990	53.84%	-0.157	-0.266	-0.050
78.75	415780	***	7.91E-06	904	1055	56.40%	-0.265	-0.372	-0.159
90	406350	***	2.51E-06	915	1026	56.72%	-0.284	-0.394	-0.176

678 *Note. Refer to Table 2 note.*

679

680 *Table 3: Target Side, U-tests over distances for a distractor frequency effect (F-20 against F-80):*

Distance	U-stat		p-value	n.F8	n.F2	CLES	HLA	95% CI	
11.25	225235	***	2.52E-05	1550	346	58.00%	-0.192	-0.273	-0.111
22.5	259148	**	1.35E-03	1516	390	56.17%	-0.202	-0.309	-0.097
33.75	252640	.	5.10E-02	1555	358	54.62%	-0.193	-0.332	-0.055
45	228095	***	3.26E-05	1566	346	57.90%	-0.384	-0.549	-0.219
56.25	245242	***	7.39E-04	1565	361	56.59%	-0.297	-0.449	-0.148
67.5	279013		6.15E-01	1625	365	52.96%	-0.126	-0.268	0.014
78.75	267306		1.00E+00	1536	357	51.25%	-0.051	-0.186	0.085
90	287083		1.00E+00	1525	363	48.14%	0.074	-0.059	0.207

681 *Note. Refer to Table 2 note.*

682

683 *Table 4: Distractor Side, U-tests over distances for a distractor frequency effect (F-20 against F-80):*

Distance	U-stat		p-value	n.F8	n.F2	CLES	HLA	95% CI	
11.25	376754	**	4.34E-03	1556	437	44.59%	0.142	0.062	0.222
22.5	344744	**	4.80E-03	1582	392	44.41%	0.176	0.076	0.275
33.75	360737	*	1.44E-02	1538	427	45.07%	0.198	0.074	0.320
45	387352	***	1.15E-05	1537	438	42.46%	0.356	0.210	0.503
56.25	323915		1.00E+00	1517	414	48.42%	0.069	-0.069	0.208
67.5	299833		1.00E+00	1451	408	49.35%	0.027	-0.105	0.158
78.75	302211		1.29E-01	1532	427	53.80%	-0.154	-0.281	-0.028
90	295816		1.00E+00	1540	401	52.10%	-0.090	-0.226	0.047

684 *Note. Refer to Table 2 note.*

685

686

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