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**In the corner of the eye: camouflaging motion in the peripheral visual field**

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20 **Abstract**

21 Most animals need to move, and motion will generally break camouflage. In many instances,  
22 most of the visual field of a predator does not fall within a high-resolution area of the retina  
23 and so, when an undetected prey moves, that motion will often be in peripheral vision. We  
24 investigate how this can be exploited by prey, through different patterns of movement, to  
25 reduce the accuracy with which the predator can locate a cryptic prey item when it  
26 subsequently orients towards a target. The same logic applies for a prey species trying to  
27 localise a predatory threat. Using human participants as surrogate predators, tasked with  
28 localising a target on peripherally viewed computer screens, we quantify the effects of  
29 movement (duration and speed) and target pattern. We show that, while motion is certainly  
30 detrimental to camouflage, should movement be necessary, some behaviours and surface  
31 patterns reduce that cost. Our data indicate that the phenotype that minimises localisation  
32 accuracy is unpatterned, having the mean luminance of the background, does not utilise a  
33 startle display prior to movement, and has short (below saccadic latency), fast movements.

34 [182 words]

35

36 **Keywords:** Motion camouflage; defensive coloration; visual search; peripheral vision;  
37 position perception

## 38 1. Introduction

39 If motion breaks camouflage [1, 2], exploring the determinants of detection of a single  
40 moving target in central vision can be considered trivial. However, the peripheral visual field  
41 is generally a region of diminished resolution [3], so detection of motion need not guarantee  
42 successful targeting of a prey that subsequently stops and resumes crypsis. Localisation of a  
43 camouflaged target in the periphery is arguably a more ecologically valid characterisation of  
44 the early stages of predation than testing detection ability within central vision: there is a low  
45 probability that a predator will be looking directly at a concealed prey item at the moment  
46 that it starts to move and, by the time attention is focused on the prey, it may have stopped  
47 moving and returned to a static camouflaged state. The same holds true for a prey trying to  
48 locate a stalking predator.

49 Previous research on camouflage has focussed predominantly upon the effectiveness of  
50 strategies in the absence of motion [4-7], although see [8]. Camouflage operates by  
51 exploiting a predator's perceptual system, making detection difficult (*e.g.* by reducing the  
52 signal at the stage of lower-level visual processing), and/or manipulating a predator's  
53 cognitive mechanisms so that identification is difficult (acting at a higher-level of information  
54 processing) [6, 7, 9]. Movement, a salient cue, allows an observer to segregate an object  
55 from the background through relative motion information [10, 11]. Movement appears to be  
56 incompatible with camouflage, resulting in the general consensus that motion breaks  
57 camouflage [1, 2, 8]. However, an organism must often move, whether to get to a point of  
58 refuge, a feeding site, or a mating prospect.

59 Here, using human observers, we investigate a common situation when predators are  
60 foraging but have yet to detect a prey item, or a prey item is vigilant in the face of predation  
61 risk: the target is most likely to be detected, via its motion, in the predator's peripheral visual  
62 field, with attention subsequently brought to bear on it [12]. Localising and responding to a  
63 stimulus in the periphery is complicated by the need to take into account cortical  
64 transmission and processing delays, as well as those associated with the preparation and

65 execution of motor actions [13]. Studies on humans suggest that the perceived position of a  
66 moving target is predicted via motion extrapolation, and that localisation is affected by the  
67 time it takes for the observer to move their eyes toward the target (i.e. the saccadic latency)  
68 [13]. Many species use saccades alongside fixations to perceive their environment; typically,  
69 these are eye-saccades but can also be head-saccades, in the case of birds, or body-  
70 saccades, in the case of insects [14]. Furthermore, many species have a region of the visual  
71 field that has a high concentration of cone photoreceptors (*e.g. area centralis*) [see 14, 15;  
72 table 3 pg. 187], giving good visual acuity; as eccentricity from this region increases  
73 photoreceptor density, and thus acuity, decreases. Amongst other things, the fixate-saccade  
74 strategy allows an organism to divert the higher-resolution region of its visual field toward an  
75 object [14]. What prey movement strategies might minimise the probability of localisation,  
76 and does surface patterning affect this? Here, we focus on two key parameters of transient  
77 movement (duration and speed) and their interaction with surface pattern. In addition, we  
78 included a flash manipulation, where a highly conspicuous display occurs before target  
79 movement. Some, otherwise cryptic, insects reveal conspicuous underwings when they fly.  
80 These are usually considered to be displays that startle a predator or interfere with  
81 identification [16-19] when the predator has already detected the prey and is initiating an  
82 attack. Here, we explore a different possible advantage that occurs when prey movement  
83 occurs in peripheral vision: gaze may be 'anchored' upon the initial location by a highly  
84 salient but transient display, and subsequent movement masked due to a flash-lag effect  
85 [20] or sensory overload [21]. Instead of exploring the effectiveness of motion camouflage  
86 strategies with regards to impeding capture, as in motion dazzle experiments [22-28], we  
87 aim to explore the phenotype's effects on localisation.

## 88 **2. Methods**

### 89 **(a) Setup**

90 The control program was written in Matlab (The Mathworks Inc. Natick, MA) with the  
91 Psychophysics Toolbox extensions [29-31]. The experiment used two gamma-corrected

92 21.5" iiyama ProLite B2280HS monitors (Iiyama; Hoofddorp Netherlands), with a refresh rate  
93 of 60 Hz, a resolution of 1200 x 1080 pixels, and a mean luminance of 64 cd/m<sup>2</sup>, controlled  
94 by an iMac (Apple; California, US). The screens were positioned so that the centre of each  
95 one was 50 cm from the subject and at an angle of 65° from a fixation cross on a third, not  
96 gamma corrected, central screen. At 50 cm each pixel subtended 1.7 arcmin.

97 During each trial, the participant was shown a square target (48 x 48 pixels), which  
98 appeared, moved, and then disappeared. Targets could appear on either the left or right  
99 screen (the central screen only displayed the fixation cross). The target moved in a  
100 sequence that was dictated by a combination of two movement factors (duration and speed),  
101 a pattern factor (see figure 1), and a flash factor (see below for details). Within each trial the  
102 target would move on a background generated by a 1/f function [32], representing a generic  
103 textured background to which visual systems are hypothesised to be adapted [33]. Spectral  
104 analysis of natural scenes shows that amplitude is inversely related to spatial frequency,  $f$ ;  
105 hence the 1/f function [33]. The background was generated afresh every trial. After a random  
106 latency (a uniform distribution from 1-3 s, in 0.5 s increments), the target appeared in the  
107 centre of one of the two screens at random (probability 0.5), and then moved in a random  
108 direction (discrete uniform distribution in the range 1-360°) in a manner determined by the  
109 factorial combination of factors described below. The target then disappeared, the non-target  
110 screen turned plain grey and the cursor appeared in the centre of the target screen, which  
111 retained its 1/f background. In this way, it was unambiguous to the participant on which  
112 screen the target had moved; the task was to localise where it had stopped.

113 Duration of movement (*duration*) had three levels that were designed to bracket saccadic  
114 latency for our human observers [34]: 100, 200 & 400 ms. Speed had three levels that were  
115 designed to provide a range of velocities (relatively slower and relatively faster) around data  
116 on movement speeds of *Zootoca vivipara* [see 35]: 10, 20 and 35 deg/s. A speed of 35,  
117 rather than 40 deg/s, was chosen so that targets always remained on the screen. Patterning  
118 had three levels (figure 1): black (*Black*; luminance = 0 cd/m<sup>2</sup>), grey (*meanLum*; luminance =

119 64 cd/m<sub>2</sub>) and background matching (*BG*; *1/f* function, luminance = 66 cd/m<sub>2</sub>). The  
120 background matching function used the same algorithm as that which created the  
121 background. Finally, the target could flash briefly prior to movement (maximum luminance =  
122 113cd/m<sub>2</sub>). This flash factor had three levels: display for 80 ms, 50 ms or not presented at  
123 all. The flash was designed to simulate a startle display [16]. It was added prior to movement  
124 to explore its putative effect on masking the target's end location.

### 125 **(b) Task**

126 After the target had finished moving and disappeared, participants clicked a mouse-  
127 controlled on-screen cursor (an 8-pixel radius red circle) on the target's estimated final  
128 location. The locations of the centre of the target and the cursor were recorded every frame.  
129 On each trial, localisation error was computed as the pixel distance between the centre of  
130 the target at its final location and the centre of the cursor at the location where it was clicked.  
131 The response time for the participant to click the cursor, from the moment at which the target  
132 started moving, was also recorded for each trial. Each participant completed six practice  
133 trials followed by 162 test trials, which were broken into three blocks of 54. Therefore,  
134 participants received all conditions (3 x 3 x 3 x 3) on both screens. Participants were free to  
135 take a break between blocks but, in practice, seldom paused for more than a few seconds.  
136 The combination of movement and pattern for each trial was independently randomised for  
137 every participant. Each trial was completed with the room lights off and with headphones on  
138 (to minimise distractions). There were 18 unpaid participants (10 female, ages 18-28), with  
139 normal/corrected-to-normal vision, who were naïve to the aims of the experiment. Ethical  
140 approval was obtained through the Faculty of Science Research Ethics Committee of the  
141 University of Bristol. All participants were briefed and gave their informed written consent, in  
142 accordance with the Declaration of Helsinki.

### 143 **(c) Statistical analyses**

144 Statistical analyses were performed using R (R Foundation for Statistical Computing,  
145 [www.R-project.org](http://www.R-project.org)). Both pixel error (*error*) and response time (*RT*) were distributed log-

146 normally, and so were log<sub>10</sub>-transformed prior to fitting linear mixed models [function lmer in  
147 the lme4 package: 36]. Participant was fitted as a random effect, with fixed effects *speed*,  
148 *duration*, *pattern*, *screen* and *flash*. Initially all fixed main effects and their interactions were  
149 fitted, followed by backwards stepwise elimination of non-significant terms (based on  
150 likelihood ratio tests), starting with the highest order interactions (see electronic  
151 Supplementary Material). Within-factor effects were explored using Tukey-type p-values [R  
152 package multcomp: 37].

### 153 **3 Results**

154 Four extremely short response times (under 0.3 s) were outliers (> 5 standard deviations  
155 from the mean on the log-transformed scale, when the next lowest was 1.5 standard  
156 deviations) and from one participant; these were considered to be premature, accidental,  
157 mouse clicks. Five data points were also considered to be response errors because the  
158 mouse click was off the target screen (possible, as the mouse could be moved to the central  
159 and non-target screens). These nine values comprised only 0.3% of the data and were  
160 removed. Localisation error is the primary response variable, but a detailed analysis of  
161 response times can be found in the Supplementary Material.

162 For localisation error, the final model showed significant main effects of the *flash* factor ( $\chi^2 =$   
163 7.44, df = 2, p = 0.0242), and screen side ( $\chi^2 = 5.84$ , df = 1, p = 0.0157), on the participant's  
164 localisation accuracy, with no interactions between these and other factors (Fig. 2 and  
165 Supplementary Material). Tukey-type pair-wise tests indicated that no flash had a  
166 significantly larger error than a flash of 50 ms (z = 2.388, p = 0.0446) and a similar, but non-  
167 significant, difference from an 80 ms flash (z = 2.325, p = 0.0523); 50 ms and 80 ms flashes  
168 were not significantly different (z = 0.063, p = 0.9978). The effects of the *flash* factor can be  
169 seen in figure 2. The main effects of *screen* showed a slightly (2.7%) lower localisation error  
170 on the right screen, which suggests a bias that could be attributed to eye preference [38].



171 Additionally, the model showed that there were significant interactions between the duration  
172 of movement and the speed of movement ( $\chi^2 = 11.00$ ,  $df = 4$ ,  $p = 0.0266$ ), and the duration  
173 of movement and the pattern on the target ( $\chi^2 = 11.24$ ,  $df = 4$ ,  $p = 0.0240$ ). To understand  
174 these interactions, the data were split by the factor *duration* and the effects of speed and  
175 pattern assessed for each level. At the shortest duration, 100 ms, there was no significant  
176 effect of pattern (Fig. 2;  $\chi^2 = 1.30$ ,  $df = 2$ ,  $p = 0.5219$ ), but at 200 ms there was ( $\chi^2 = 10.75$ ,  $df$   
177  $= 2$ ,  $p = 0.0046$ ), with mean luminance having the greatest error, significantly greater than  
178 black ( $z = 3.28$ ,  $p = 0.0030$ ), but not background matching ( $z = 1.75$ ,  $p = 0.1872$ ). Black and  
179 background matching did not differ ( $z = 1.52$ ,  $p = 0.2802$ ). At 400 ms there was also a  
180 significant effect of pattern ( $\chi^2 = 19.39$ ,  $df = 2$ ,  $p < 0.0001$ ), mean luminance again having  
181 the greatest error, significantly greater than black ( $z = 4.41$ ,  $p < 0.0001$ ), but not background  
182 matching ( $z = 2.047$ ,  $p = 0.1013$ ). Background matching also had a greater error than black  
183 ( $z = 2.371$ ,  $p = 0.0467$ ). Regarding the interaction between duration and speed, at 100 ms  
184 there was a significant effect of speed ( $\chi^2 = 22.39$ ,  $df = 2$ ,  $p < 0.0001$ ), with a greater error  
185 for 35 deg/s than for 10 or 20 deg/s ( $z = 4.60$ ,  $p < 0.0001$  and  $z = 3.34$ ,  $p = 0.0024$   
186 respectively); 10 and 20 deg/s did not differ ( $z = 1.26$ ,  $p = 0.4155$ ). At 200 ms there was also  
187 a significant effect of speed ( $\chi^2 = 34.69$ ,  $df = 2$ ,  $p < 0.0001$ ), error increased progressively  
188 with speed (Fig.2; 10 vs 20 deg/s:  $z = 2.47$ ,  $p = 0.0364$ ; 20 vs 35 deg/s:  $z = 3.44$ ,  $p = 0.0017$ ;  
189 10 vs 35 deg/s:  $z = 5.91$ ,  $p < 0.0001$ ). At 400 ms there was also a significant effect of speed  
190 ( $\chi^2 = 16.93$ ,  $df = 2$ ,  $p = 0.0002$ ), with a greater error for 20 and 35 deg/s than for 10 deg/s ( $z$   
191  $= 3.83$ ,  $p < 0.0001$  and  $z = 3.25$ ,  $p = 0.0033$  respectively); 20 and 35 deg/s did not differ ( $z =$   
192  $0.57$ ,  $p = 0.8355$ ).

193 Modelling for response time indicated a significant interaction between pattern and flash  
194 when the stimulus moved for 100 ms, with pattern only having a significant effect in the no  
195 flash condition (Supplementary Material). Specifically, mean luminance had longer response  
196 times than background matching or black patterning, which did not differ. At 200 ms there  
197 was a significant effect of flash, with the no flash condition having a longer response time

198 than the flash conditions. At 400 ms there was a significant effect of speed, where an  
199 increase in speed increased the response time.

#### 200 **4. Discussion**

201 Unless already detected and fixated, a prey item seeking to avoid a predator, or a predator  
202 seeking to approach prey undetected, is likely to be moving within the peripheral visual field.  
203 Our data indicate that for such a moving target to minimise its localisation, it should move  
204 briefly and quickly, and it should be unpatterned, with similar luminance to the background. A  
205 first-order stimulus is defined by intensity differences between target and background, while  
206 a second-order stimulus is defined by a difference in some other property, (*e.g.* contrast or  
207 pattern). Matching the mean luminance of the target and background pushes the stimulus  
208 towards being second-order, and is well known that such stimuli are far weaker than their  
209 first-order counterparts [*e.g.* 39, 40]. A conspicuous flash, such as a startle display, prior to  
210 movement does not anchor the predator's saccade to the initial location. In fact, it is  
211 detrimental: localisation errors are slightly lower and, for short motion durations, response  
212 times considerably shorter, if motion is preceded by a flash. In all treatments, the estimated  
213 direction of the target's motion was usually judged fairly accurately, but participants overshoot  
214 its stopping place (Supplementary Material), for the most difficult targets by more than three  
215 body lengths (Figure 2; a 150+ pixel error when the width of the target is 48 pixels). This sort  
216 of biased error is frequently observed in motion estimation tasks and is known as  
217 representational momentum [13, 41]. In our experiment, greater speed led to greater  
218 overshoot, particularly for short duration movements (Fig. 2).

219 Brief movement was the best strategy to increase localisation error, with the greatest errors  
220 happening when the duration was shorter than the saccadic latency (100-200 ms) [15, 34,  
221 42-45]. Little information is gathered whilst the eyes are saccading [46], and thus stopping  
222 before a viewer has had time to complete a saccade and fixate is advantageous.

223 Considering that the fixate-saccade strategy is ubiquitous, this suggests that the prevalence  
224 of the intermittent motion observed in many animals [35, 47-54], which is often attributed to

225 the benefits of image stabilisation for the prey species itself [35, 52, 53, 55], could instead (or  
226 additionally) serve to reduce a predator's ability to localise a prey [35, 52]. Avery *et al.* [35]  
227 has shown that in the lizard *Zootoca vivipara*, normal movement operates in bursts that  
228 broadly correspond to human saccadic latency and, further, a movement speed that  
229 approximately corresponds to 20 deg/s. In organisms that are successful at stationary  
230 camouflage, can change colour [56], or have different appearances through a "flicker-fusion"  
231 effect [57], saltatory locomotion could be particularly advantageous. In our experiment, the  
232 phenotype that induced the greatest localisation error was plain, with the mean luminance of  
233 the background, rather than background-matching in pattern. Cuttlefish that are camouflaged  
234 when stationary have been observed to change to a plain colour when moving [56],  
235 consistent with what we would predict from our results. Although, for short (100 ms) duration  
236 movements, the pattern of the target had no effect on localisation error (Fig. 2), this was at  
237 the cost of a far longer response time in the absence of an alerting flash.

238 Our data show that it is more advantageous to move quickly to reduce localisation accuracy  
239 [24]. This seems counter to the typical slow movements used by military operatives [58, 59]  
240 and stalking predators [60] and could suggest an alternative; namely, darting between  
241 periods of stationary camouflage or refuges/protective cover. There is a significant  
242 interaction between the movement duration and the target's movement speed, with  
243 increased speed above 20 deg/s having no additional benefit for 400 ms movements.

244 However, this could be an artefact of targets nearing the screen edge in the fast/long-  
245 duration combination of treatments, such that the extent of over-estimation was constrained.

246 A flash before movement does not 'anchor' the viewer's fixation upon the target's starting  
247 point. Instead, it appears that the flash cues the viewer to divert their attention towards the  
248 target and primes them for the motion that follows, and could hence accelerate the saccade  
249 to locate the target in central vision [61]. This contradicts multiple accounts in the literature  
250 that deem highly salient patterns as having a startle effect [62-66]; these are proposed to  
251 operate by overloading the perceptual mechanisms of the predator with sensory information,

252 so that a prey animal can escape [21]. However, in the current study the target appears in  
253 peripheral vision, away from the focus of attention, and so a startle effect would be unlikely.  
254 Also, our results do not support the idea that motion, and subsequent localisation, is masked  
255 due to a flash-lag effect. This is likely due to motion continuing beyond the flash-lag  
256 processing time and, in order to be effective, flashing should correspond with cessation of  
257 movement [17, 18].

258 The response time data support the conclusions of localisation error, indicating that shorter  
259 durations with mean luminance patterning and no flash prior to movement take longer to  
260 localise. Target speed had a limited effect on response time when durations were short, but  
261 response time increased progressively with target speed when the duration of movement  
262 was longer (400 ms), indicating increased uncertainty even when the moving target was in  
263 central vision.

264 Whilst motion is certainly detrimental to camouflage [1, 2] should movement be necessary  
265 some behaviours and surface colour patterns reduce that cost [56]. Within the parameters  
266 set by our experiment, the phenotype that minimises detection and localisation is  
267 unpatterned, has mean background luminance, does not utilise a startle display (no flash)  
268 prior to movement, and has short (below saccadic latency), fast movements. It is feasible  
269 that predator attention is drawn to the first instance of movement and, subsequently,  
270 predators could sit-and-wait for additional movement. However, this presupposes that the  
271 predator was able to recognise the source of movement as potential prey, which may not be  
272 the case. Additionally, it may not be beneficial for the predator to sit-and-wait for subsequent  
273 movement from an uncertain source; continuing to actively search the environment may be  
274 more beneficial. Furthermore, we must consider how noisy environments can be (e.g. foliage  
275 in the wind) and the impact that this may have upon localisation of a moving target [8]. This  
276 experiment highlights the importance of addressing ecological problems, whilst also  
277 considering the perceptual differences that different regions of the visual field permit. Whilst  
278 there are almost certainly quantitative differences across species, the qualitative effects

279 should remain the same. If we consider the ubiquity of the fixate-saccade strategy [14], and  
280 the distribution of photoreceptors that results in a high-resolution region surrounded by an  
281 area where resolution drops with increasing eccentricity, we could expect these results to  
282 occur in many other species. So, while the speed and mechanism (eye, head or body  
283 movement) will no doubt differ between humans and other species, the pattern of results  
284 should hold generally. In particular, because limited information is acquired during a viewer's  
285 gaze shift, to reduce the probability of being located accurately an animal should move and  
286 stop before it can be fixated, and limit the amount of visual information available while  
287 moving with colouration that approximates the mean luminance of the background and lacks  
288 patterning. It would be very difficult to carry out similar experiments with non-human  
289 subjects; we chose humans because it allowed us to be very specific in what we required  
290 our observers to do, and what we measured. Our results show that the ability of a (model)  
291 predator to localise a target presented in peripheral vision is influenced by different  
292 components of movement (duration and speed) and target pattern; motion does not always  
293 break camouflage.

#### 294 **Ethics**

295 Participants gave their informed written consent in accordance with the Declaration of  
296 Helsinki, and the Ethical Committee of the Faculty of Science, University of Bristol, approved  
297 the experiment.

#### 298 **Data accessibility**

299 All data are available from Dryad doi: to be completed upon publication.

#### 300 **Authors' contributions**

301 All authors conceived and designed the experiment; I.E.S. and N.S.S. programmed the  
302 experiment; I.E.S. carried out the experiment; I.E.S. and I.C.C. analysed the data; I.E.S.  
303 wrote the first draft of the manuscript with subsequent contributions by all authors.

304 **Competing interests**

305 The authors declare no competing interests.

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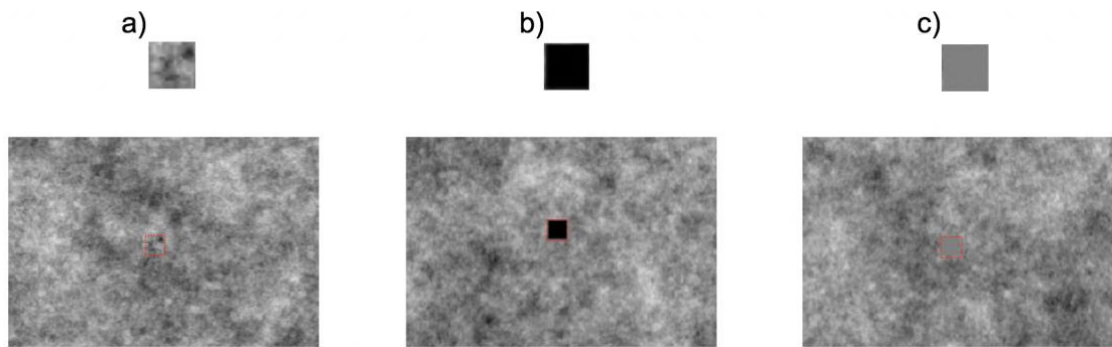
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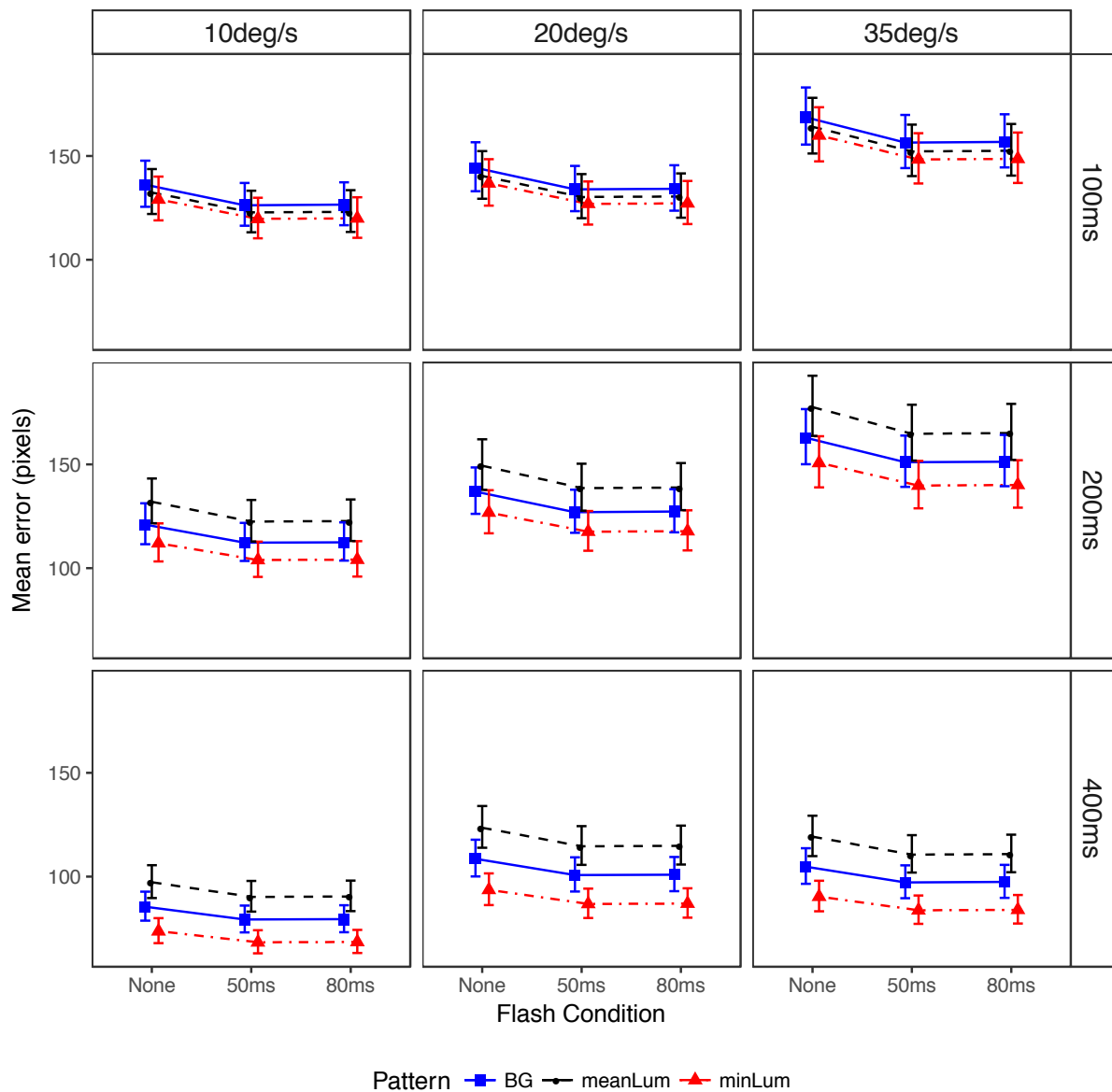
475 **Figures**



476

477 Figure 1 - The target patterning that was used (a) background matching, created using  
478 a  $1/f$  function; (b) black; (c) grey (mean luminance). Below each target is an example of  
479 how the target would appear on a background. A red outline has been added to  
480 highlight the position of the target on the background (not present during the  
481 experiment).

482



484

485 Figure 2 - The mean error associated with the participant's ability to localise a moving object  
 486 with different movement and patterning conditions, with 95% confidence intervals based on  
 487 the fitted model (N=18 participants). Different combinations of movement and patterning  
 488 conditions can be navigated via the panelling. The phenotype with the strongest effect has  
 489 mean luminance, does not utilise a flash and has short, fast movements. Further, note that  
 490 the width of the target is 48 pixels, and therefore the aforementioned phenotype is missed by  
 491 more than three body lengths.

## Smart et al. Supplementary Material

Table S1. Location error: model simplification steps, starting with a full model (five fixed effects and all possible interactions).

Step	Term removed	$\chi^2$	df	p
1	Flash:Pattern:Screen:Duration:Speed	13.77	16	0.6161
2	Flash:Screen:Duration:Speed	3.36	8	0.9095
3	Flash:Pattern:Duration:Speed	11.05	16	0.8062
4	Flash:Pattern:Screen:Speed	4.59	8	0.8002
5	Flash:Pattern:Speed	1.68	8	0.9894
6	Flash:Pattern:Screen:Duration	7.66	8	0.4672
7	Flash:Screen:Duration	0.12	4	0.9983
8	Flash:Pattern:Screen	1.22	4	0.8749
9	Flash:Pattern:Duration	5.61	8	0.6913
10	Flash:Duration:Speed	9.62	8	0.2931
11	Flash:Duration	1.24	4	0.8723
12	Flash:Pattern	5.40	4	0.2484
13	Flash:Screen:Speed	6.30	4	0.1780
14	Flash:Screen	0.28	2	0.8697
15	Flash:Speed	2.63	4	0.6222
16	Pattern:Screen:Duration:Speed	11.53	8	0.1737
17	Pattern:Screen:Duration	0.89	4	0.9259
18	Pattern:Duration:Speed	5.16	8	0.7401
19	Screen:Duration:Speed	4.24	4	0.3746
20	Screen:Duration	1.33	2	0.5134
21	Pattern:Screen:Speed	8.85	4	0.0650
22	Screen:Speed	0.33	2	0.8489
23	Pattern:Screen	1.11	2	0.5741
24	Pattern:Speed	7.45	4	0.1139

The initial (saturated) model was  $\sim$  Flash\*Pattern\*Screen\*Duration\*Speed + (1 | Subject). Significance was assessed using likelihood ratio tests.

## Analysis of response time

The final model contained a significant two-way interaction between duration and speed ( $\chi^2 = 29.88$ ,  $df = 4$ ,  $p < 0.0001$ ), and a three-way interaction between duration, pattern and the flash prior to the target moving ( $(\chi^2 = 21.74$ ,  $df = 8$ ,  $p = 0.0054)$  (Fig. S1; Table S2). To explore the nature of these interactions the data were split by duration, and models fitted with speed, pattern, flash and the two-way interaction between the latter two factors. For 100 ms movements, speed was not significant ( $\chi^2 = 0.67$ ,  $df = 2$ ,  $p = 0.7150$ ), but the pattern x flash interaction was ( $\chi^2 = 26.14$ ,  $df = 4$ ,  $p < 0.0001$ ). Analysing the flash conditions separately, with no flash, pattern was significant ( $\chi^2 = 26.29$ ,  $df = 2$ ,  $p < 0.0001$ ), with the mean luminance pattern having longer response times than black ( $z = 4.70$ ,  $p < 0.0001$ ) and background matching ( $z = 4.32$ ,  $p < 0.0001$ ), with the latter two treatments not differing ( $z = 0.40$ ,  $p = 0.9170$ ). However, when movement was preceded by a flash, there was no significant effect of pattern (50 ms:  $\chi^2 = 2.75$ ,  $df = 2$ ,  $p = 0.2530$ ; 80 ms:  $\chi^2 = 0.16075$ ,  $p = 0.9228$ ).

For 200 ms movements, the pattern:flash interaction was not significant ( $\chi^2 = 3.33$ ,  $df = 4$ ,  $p = 0.5039$ ). So, removing this term and simplifying the model sequentially, neither pattern ( $\chi^2 = 4.79$ ,  $df = 2$ ,  $p = 0.0914$ ) or speed ( $\chi^2 = 5.58$ ,  $df = 2$ ,  $p = 0.0613$ ) were significant, but flash was ( $\chi^2 = 35.03$ ,  $df = 2$ ,  $p < 0.0001$ ), with response times longer for no flash than when a flash preceded movement (no flash vs 50 ms flash:  $z = 4.28$ ,  $p < 0.0001$ ; no flash vs 80 ms flash:  $z = 5.74$ ,  $p < 0.0001$ ; 50 ms vs 80 ms flash:  $z = 1.46$ ,  $p = 0.3080$ ).

For 400 ms movements, the pattern x flash interaction was not significant ( $\chi^2 = 4.10$ ,  $df = 4$ ,  $p = 0.3927$ ). So, removing this term and simplifying the model sequentially, neither pattern ( $\chi^2 = 0.48$ ,  $df = 2$ ,  $p = 0.7865$ ) or flash ( $\chi^2 = 4.95$ ,  $df = 2$ ,  $p = 0.0841$ ) were significant, but speed was ( $\chi^2 = 70.92$ ,  $df = 2$ ,  $p < 0.0001$ ), with response times increasing with target speed (10 vs 20 deg/s:  $z = 3.565$ ,  $p = 0.0011$ ; 10 vs 35:  $z = 8.53$ ,  $p < 0.0001$ ; 20 vs 35:  $z = 4.98$ ,  $p < 0.0001$ ).



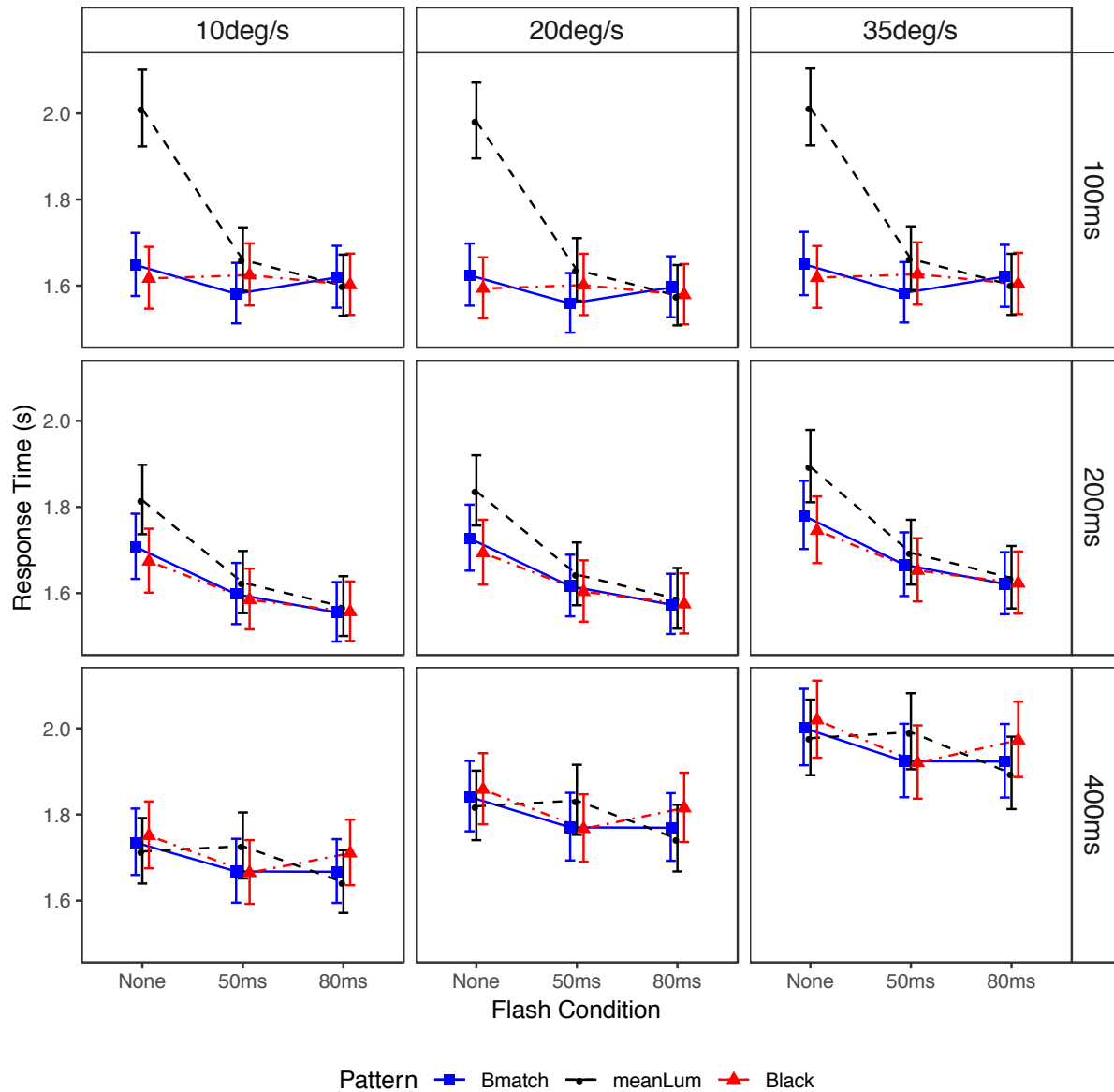


Figure S1 - The response time for participants trying to localise a moving object with different movement and patterning conditions, with 95% confidence intervals based on the fitted model (N=18 participants). Different combinations of movement and patterning conditions can be navigated via the panelling. The phenotype with the strongest effect has mean luminance, does not utilise a flash and has short and/or fast movements.

Table S2. Response time: model simplification steps, starting with a full model (five fixed effects and all possible interactions).

Step	Term removed	$\chi^2$	df	p
1	Flash:Pattern:Screen:Duration:Speed	16.29	16	0.4333
2	Flash:Screen:Duration:Speed	2.26	8	0.9720
3	Pattern:Screen:Duration:dotShift	5.67	8	0.6846
4	Pattern:Screen:Duration	1.22	4	0.8746
5	Flash:Pattern:Duration:dotShift	13.46	8	0.6389
6	Pattern:Duration:dotShift	4.27	8	0.8321
7	Flash:Screen:Duration:dotShift	9.86	8	0.2749
8	Flash:Screen:Duration	1.21	4	0.8756
9	Screen:Duration:dotShift	3.27	8	0.5130
10	Screen:Duration	0.35	2	0.8375
11	Flash:Duration:dotShif	11.36	4	0.1821
12	Flash:Pattern:Screen:dotShift	13.94	4	0.0835
13	Flash:Pattern:Screen	2.95	4	0.5655
14	Flash:Pattern:dotShift	9.11	8	0.3331
15	Pattern:Screen:dotShift	5.75	4	0.2187
16	Pattern:Screen	1.32	2	0.5165
17	Pattern:dotShift	7.67	4	0.1046
18	Flash:Screen:dotShift	8.04	4	0.0902
19	Flash:Screen	0.21	2	0.9018
20	Screen:dotShift	3.51	2	0.1725
21	Screen	0.03	1	0.8599
22	Flash:dotShift	7.55	4	0.1096

The initial (saturated) model was  $\sim$  Flash\*Pattern\*Screen\*Duration\*Speed + (1 | Subject). Significance was assessed using likelihood ratio tests.

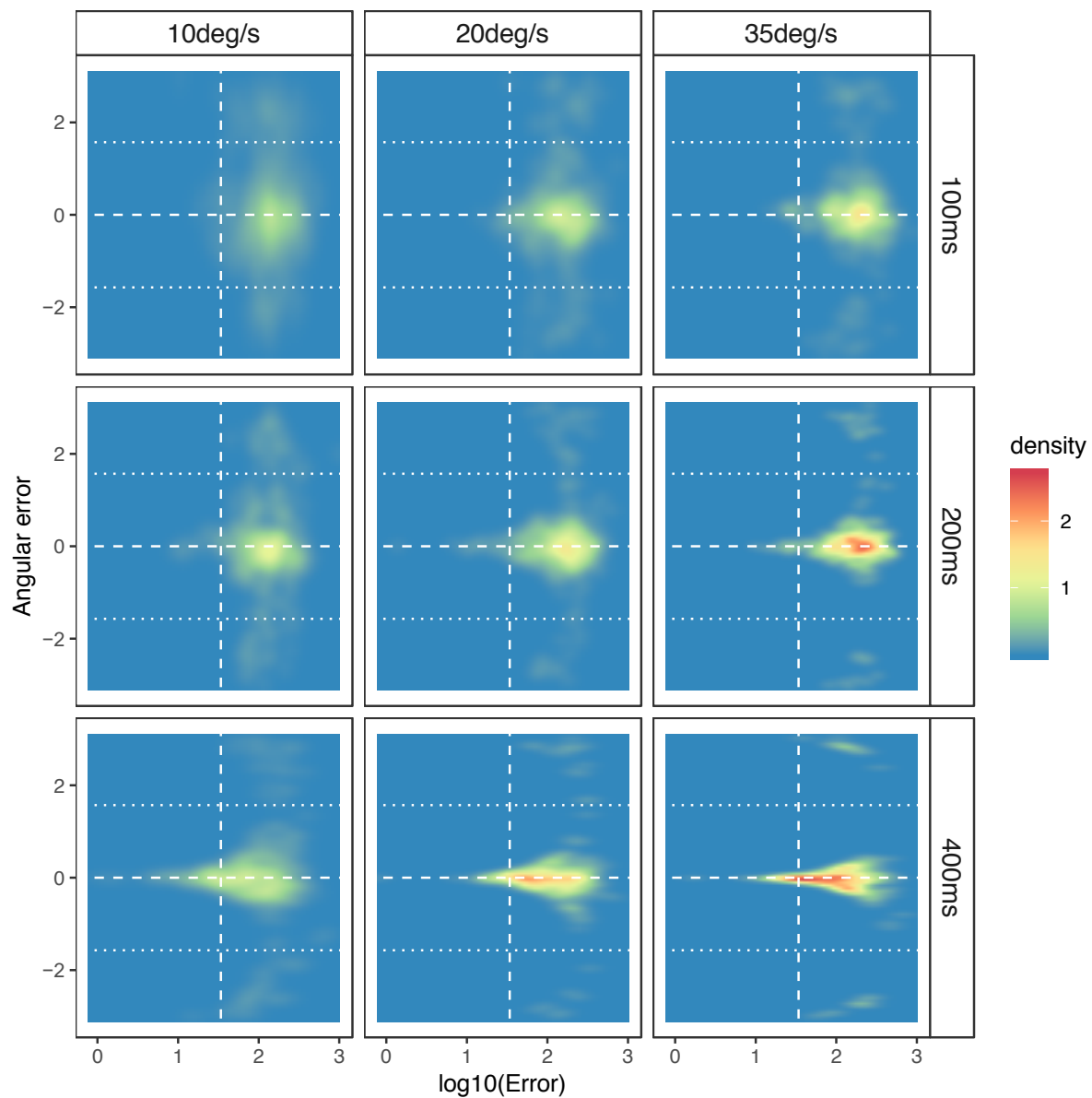


Figure S2 – Angular error (relative to the target’s trajectory) plotted against the log-transformed localisation error (distance from target) in pixels for participants trying to localise a moving object with different movement and patterning conditions (N=18 participants). Different combinations of movement and patterning conditions can be navigated via the panelling.