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Published in:
Vision Research

DOI:
[10.1016/j.visres.2019.03.005](https://doi.org/10.1016/j.visres.2019.03.005)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Early version, also known as pre-print

Publication date:
2019

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Pilz, K. S., & Papadaki, D. (2019). An advantage for horizontal motion direction discrimination. *Vision Research*, 158, 164-172. <https://doi.org/10.1016/j.visres.2019.03.005>

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1 **An advantage for horizontal motion direction discrimination**

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34

35 **Abstract**

36 Discrimination performance is better for cardinal motion directions than for oblique ones, a
37 phenomenon known as the oblique effect. In a first experiment of this paper, we tested the
38 oblique effect for coarse motion direction discrimination and compared performance for the
39 two cardinal and two diagonal motion directions.

40 Our results provide evidence for the oblique effect for coarse motion direction discrimination.
41 Interestingly, the oblique effect was larger between horizontal and diagonal than between
42 vertical and diagonal motion directions. In a second experiment, we assessed fine motion
43 direction discrimination for horizontal and vertical motion. It has been suggested that
44 differences in performance strongly depend on motion coherence. Therefore, we tested
45 performance at predetermined motion coherences of 30%, 40%, 50%, 60% and 70%.
46 Unsurprisingly, performance overall increased with increasing motion coherence and angular
47 deviations between control and test stimulus. More importantly, however, we found an
48 advantage for horizontal over vertical fine motion direction discrimination. Noteworthy is
49 the large variability in performance across experimental conditions in both experiments,
50 which highlights the importance of considering individual difference when assessing
51 perceptual phenomena within large groups of naïve participants.

52

53 **Keywords:** motion direction discrimination, motion perception, oblique effect, horizontal
54 motion

55

56 **1. Introduction**

57 Motion perception is an important visual ability that helps us to navigate through the
58 environment, to recognise self and object motion, and that aids social interactions. Previous
59 studies suggest that our visual system has adapted to the visual environment such that it
60 shows a preference for stimuli that are more common or more relevant. For example, it has
61 been shown that we are better at processing upright compared to inverted faces (Sekuler,
62 Gaspar, Gold, & Bennett, 2004; Tanaka & Farah, 1993) and point-light walkers (Blake &
63 Shiffrar, 2007; Pavlova, 2012; Pilz, Bennett, & Sekuler, 2010). In addition, different species,
64 including monkeys and humans show a preference for looming compared to receding stimuli,
65 which is thought to reflect their relevance to survival (Edwards & Badcock, 1993; Franconeri
66 & Simons, 2003; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004; Pilz, Vuong, Bülthoff, &
67 Thornton, 2011; Schiff, Banka, & de Bordes Galdi, 1986).

68 A preference for relevant and common visual stimuli seems to extend to the most
69 fundamental mechanisms of visual perception. For example, the perception of orientation in
70 a variety of perceptual tasks is better for cardinal than for diagonal orientations (Appelle,
71 1972; Essock, 1980; Heeley, Buchanan-Smith, Cromwell, & Wright, 1997; Orban,
72 Vandenbussche, & Vogels, 1984). This so-called oblique effect is thought to originate from
73 a prevalence of cardinal contours in our visual environment (Coppola, Purves, McCoy, &
74 Purves, 1998; Girshick, Landy, & Simoncelli, 2011). Previous studies support the hypothesis
75 that orientation perception is based on visual experience (Annis & Frost, 1973; Gwiazda,
76 Brill, Mohindra, & Held, 1978). Annis and Frost (1973), for example, investigated the
77 oblique effect in two populations that grew up in different visual environments – the Cree, a
78 group of First Nations from James Bay, Quebec, and city-raised Canadians. The authors
79 measured visual acuity for discriminating horizontal, vertical, left oblique and right oblique
80 gratings and found an oblique effect for city-raised Canadians but not the Cree. Annis and
81 Frost (1973) explain their results by the differences in occurrence of orientations in the
82 groups' visual environment. Whereas the Cree live in an environment without prominent
83 visual contours, city-raised Canadians are predominantly exposed to cardinal orientations as
84 found in carpentered environments (also see Fang, Bauer, Held, & Gwiazda, 1997; Timney
85 & Muir, 1976). Gwiazda et al., (1978) used a preferential looking paradigm to measure spatial
86 frequency thresholds for vertical and oblique gratings in infants ranging from 7-50 weeks of
87 age. They found that preference thresholds were very similar for vertical and oblique gratings
88 but increased more rapidly with age for vertical gratings. The above-mentioned studies
89 strongly support the hypothesis that the prevalence of certain orientations in our visual

90 environment has an influence on orientation perception. It is also reasonable to assume that
91 neuronal mechanisms are influenced by the incoming visual information. Many previous
92 neurophysiological studies in cats, for example, have found that the orientations within the
93 visual environment affect the orientation of receptive fields of neurons in early visual areas
94 (Barlow, 1975; Blakemore & Cooper, 1970; Hirsch & Spinelli, 1970), and it is assumed that
95 even though some orientation-specific characteristics are present at birth (Hubel & Wiesel,
96 1963), they can be influenced by visual experience (Mitchell, 1978).

97 Neuronal preferences based on visual experience have also been observed for motion
98 directions (Cynader, Berman, & Hein, 1975; Daw & Wyatt, 1976), and the oblique effect for
99 motion directions (Dakin, Mareschal, & Bex, 2005; Gros, Blake, & Hiris, 1998) seems to
100 follow similar reasoning as for orientations: the more common a motion direction is in the
101 visual environment the better its discrimination (Dakin et al., 2005). Dakin et al., (2005)
102 analysed the local statistics of natural movies for translational motion. Their finding that raw
103 energy is more broadly distributed around oblique compared to cardinal motion directions
104 supports the hypothesis that the oblique effect in motion direction discrimination is based on
105 occurrences in the visual environment (note that effects for translational motion do not
106 necessarily generalize to other motion types Edwards & Badcock, 1993).

107 In a recent paper, we extended the results on the oblique effect in motion direction
108 discrimination to differences between the two cardinal motion directions. We assessed
109 motion coherence thresholds for coarse motion direction discrimination in a comparatively
110 large sample of older and younger adults (Pilz, Miller, & Agnew, 2017), and found higher
111 motion coherence thresholds for vertical compared to horizontal motion. These results were
112 unexpected and seemed surprising at first given that they had not been described before.
113 However, previous studies assessing motion direction discrimination primarily tested
114 relatively small samples of high-performing younger adults, which might have made it
115 difficult to detect such subtle differences (Dakin et al., 2005; Gros et al., 1998).

116 A performance advantage for horizontal compared to vertical motion seems reasonable when
117 taking into account other areas in vision research, for example, relating to attention or eye-
118 movements. Within the attention literature, anisotropies between cardinal directions have
119 long been reported in that attentional deployment is facilitated along the horizontal meridian
120 (Carrasco, Talgar, & Cameron, 2001; Mackeben, 1999; Pilz, Roggeveen, Creighton, Bennett,
121 & Sekuler, 2012). In addition, smooth pursuit is more accurate and stable for horizontally
122 compared to vertically moving targets (Ke et al., 2013; Rottach et al., 1996), and gain as a
123 function of stimulus velocity decreases faster for vertical than horizontal motion (Takahashi,

124 Sakurai, & Kanzaki, 1978; van den Berg & Collewijn, 1988). It is possible that the
125 preferences for information along the horizontal compared to the vertical meridian share
126 common mechanisms that are potentially related to its relevance in our visual environment.
127 In this paper, we investigated differences in coarse and fine motion direction discrimination
128 in large samples of naïve younger participants. In a first experiment, participants were asked
129 to discriminate four coarse motion directions. Vertical (up/down), horizontal (left/right), and
130 two diagonal motion directions (lower right/upper left) and (upper right/lower left). Our
131 results provided evidence for the oblique effect: participants had lower motion coherence
132 thresholds for cardinal compared to diagonal motion directions. The oblique effect was more
133 pronounced between horizontal and diagonal motion directions than between vertical and
134 diagonal. Importantly, we found large individual differences in performance. Motion
135 direction discrimination performance has been shown to improve with increasing motion
136 coherence (Gros et al., 1998), and directional differences strongly depend on individual
137 differences in motion coherence (Pilz et al., 2017). Therefore, in a second experiment, we
138 systematically investigated the effect of coherence on performance for fine motion direction
139 discrimination. Performance for horizontal and vertical fine motion direction discrimination
140 were assessed at predefined levels of motion coherence in a between-subject design. In
141 addition to improved performance with increasing coherence and angular deviation between
142 control and test stimulus, our results showed a significant advantage for horizontal over
143 vertical fine motion direction discrimination.

144

145 **2. Experiment 1**

146

147 *2.1 Methods*

148

149 2.1.1 Participants

150 Twenty young adults (18-28 years, $M = 20.32$, $SD = 2.2$, 8 males) took part in the experiment.
151 All participants were naïve as to the purpose of the experiment and had normal or corrected-
152 to-normal vision of 0.8 or above on an Early Treatment Diabetic Retinopathy Study (ETDRS)
153 logarithmic vision chart. All participants were students of the University of Aberdeen and
154 received two credit points for their participation as part of their curriculum. The experiment
155 was approved by the local ethics committee and experiments were conducted in accordance

156 with the Code of Ethics of the World Medical Association (Declaration of Helsinki). All
157 participants gave written informed consent.

158

159 2.1.2 Apparatus

160 Experiments were conducted on an Apple Mac Mini (OS X; Apple, Inc., Cupertino, CA)
161 using the PsychToolbox extensions (Brainard, 1997; Kleiner et al., 2007) for MATLAB
162 (Mathworks, Natick, MA). Stimuli were presented on a 17-inch Viglen VL950T CRT
163 monitor (Viglen Ltd., St. Albans, Hertfordshire, UK) with a refresh rate of 100 Hz (equivalent
164 to 100 frames per second or fps) and a resolution of 1024 x 786 pixels. The apparatus was
165 similar to other experiments used in our lab (Kerr-Gaffney, Hunt, & Pilz, 2016; Miller,
166 Agnew, & Pilz, 2017; Pilz, Miller, & Agnew, 2017).

167

168 2.1.3 Stimuli

169 Stimuli were random-dot kinematograms (RDKs) similar to those described in Pilz et al.,
170 (2017) and Miller et al., (2017). RDKs were of a circular aperture of 9.4° visual angle with
171 100 dots moving at a speed of $5^\circ/s$. All dots had a size of 4 pixels and a limited lifetime of
172 200ms (equivalent to 20 frames). The dots were white and were presented on a black
173 background. The lifetime and position of each dot was randomly allocated at the beginning
174 of each trial. Once the lifetime of a dot elapsed, or the dot moved out of the stimulus region,
175 it was placed at a random position within the aperture, and set to move in the same direction
176 as before. Stimulus duration was set to 400ms while motion coherence thresholds were
177 individually determined for each participant as described below. Participants were instructed
178 to look at a fixation cross which was presented at the centre of the screen at the beginning of
179 each trial.

180

181 2.1.4 Procedure

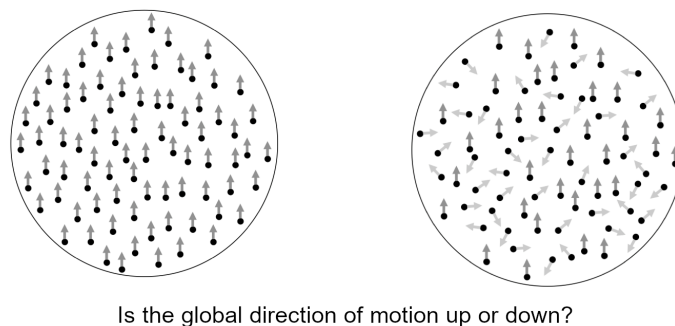
182 The Procedure was similar to Pilz et al., (2017). Participants were seated 60 cm from the
183 screen and their head position was stabilized using a chin rest. The experiment consisted of
184 four blocks of two steps each, one block each for horizontal (0°), vertical (90°), lower right
185 (315°) and upper right (45°) motion. The order of blocks was counterbalanced across
186 participants.

187 In the first step, we assessed whether participants were able to perform the task at a stimulus
188 duration of 400ms and 100% motion coherence. Participants were asked to discriminate

189 coarse motion direction on a standard QWERTY keyboard. For horizontal (left/right), upper
190 right (upper right/lower left) and lower right motion (upper left/lower right), participants
191 were asked to press “X” for left and “M” for right. For vertical (up/down) motion,
192 participants were asked to press “*” for up and “+” for down. Participants performed one
193 block of 20 trials. If accuracy was below 75% in the first block of trials, participants were
194 asked to perform another block of 20 trials. All participants were able to perform above 75%
195 correct within a maximum of two blocks of trials.

196 In the second step, we assessed the coherence level of each participant for horizontal, upper
197 right, lower right and vertical coarse motion direction discrimination using the method of
198 constant stimuli with 7 levels of motion coherence (5%, 10%, 25%, 40%, 55%, 70%, and
199 85%). The same task was used as described above. Participants completed 15 trials per
200 coherence for each motion direction, and we fit a psychometric function to assess the 82.5%
201 performance threshold for each participant. If a participant had a coherence threshold higher
202 than 100% in one of the motion directions, a value of 100% was recorded. This was the case
203 for one participants for the upper right condition and one participant for the lower right
204 condition. Data from one participant had to be excluded, because the participant only
205 performed the task for the two cardinal motion directions.

Step 1 - motion duration Step 2 - motion coherence



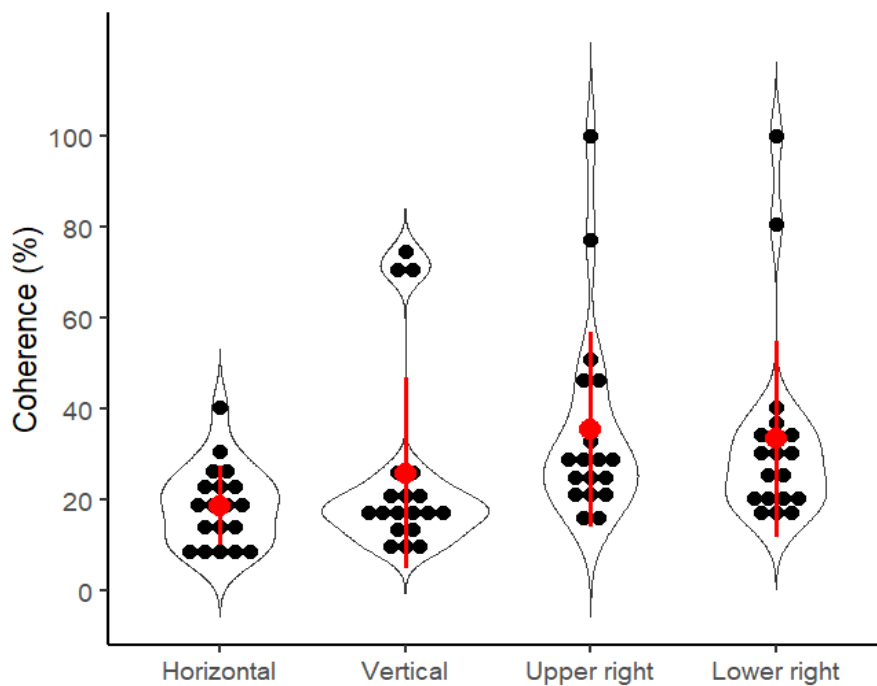
206
207 **Figure 1.** Example of stimuli and trial sequences for the two steps of the experiment for vertical motion. In step
208 1, coarse motion direction discrimination performance was assessed at a stimulus duration of 400ms and 100%
209 motion coherence. In step 2, stimulus duration was 400ms and coherence thresholds were estimated for each
210 participant individually. Participants had to determine the global direction of motion for one stimulus that
211 appeared on the screen (Figure adapted from Pilz et al., 2017).

212
213

214 2.2 Results

215 Data were analysed using RStudio (RStudio Team, 2016) and JASP (JASP Team, 2019).
 216 Individual motion coherence was assessed by the method of constant stimuli. A within-
 217 subject design was adopted to assess thresholds for the two cardinal and the two oblique
 218 motion directions (Table 1). A repeated measures ANOVA on the 82.5% thresholds showed
 219 a main effect of motion direction, $F(3,54) = 8.126$, $p < 0.01$, $\eta_p^2 = 0.193$. This was supported
 220 by a Bayesian repeated measures ANOVA that provided strong evidence for the main effect
 221 of motion direction, $BF_{10} = 172.89$. Figures 2 and 3 highlight the large individual differences
 222 in performance within and between conditions.

223



224

225 **Figure 2.** Violin plot of the motion coherence thresholds for horizontal (left/right), upper right (upper
 226 right/lower left), lower right (upper left/lower right) and vertical (up/ down) coarse motion direction
 227 discrimination with means (red dots) and standard deviations (red bars).

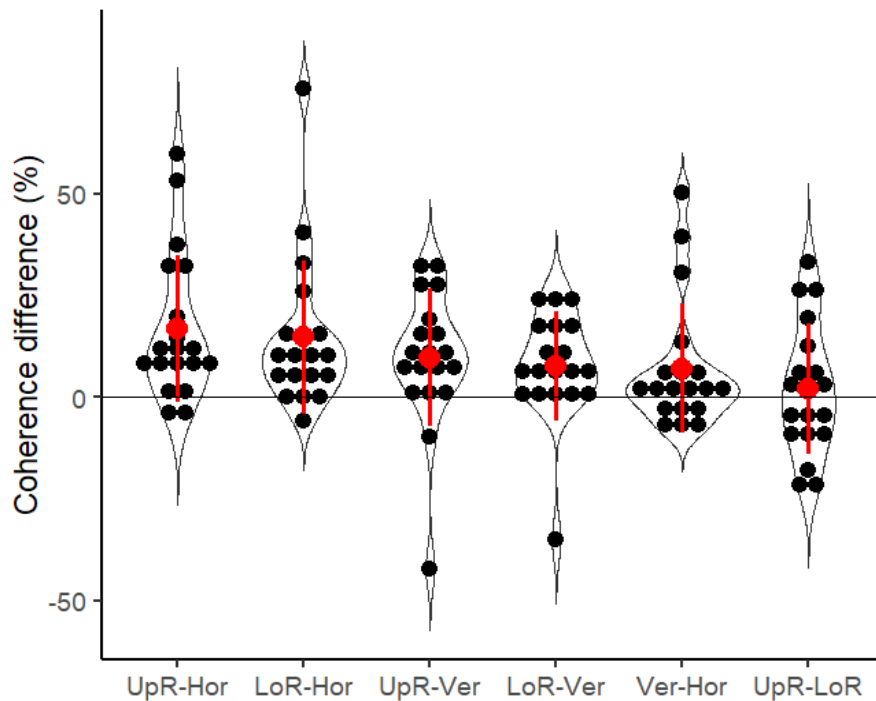
228

229 Table 1. Means (M), standard deviations (SD) and 95% bootstrapped confidence intervals (CI) for motion
 230 coherence for the four motion directions.

	M	SD	CI
Horizontal	18.7	8.68	14.91 – 22.53
Vertical	25.9	21.00	16.81 – 35.20
Upper right	35.55	21.47	26.36 – 44.60
Lower right	33.48	21.54	23.55 – 43.12

231

232 Post-hoc tests confirmed the oblique effect in that motion coherence was lower for cardinal
 233 compared to oblique motion directions (Table 2). There was no significant difference
 234 between the two oblique motion directions and between the two cardinal motion directions.
 235 Post-hoc tests were not controlled for multiple comparisons. Bayesian statistics indicate that
 236 evidence is strongest for the oblique effect being driven by horizontal thresholds, i.e., it is
 237 14.23/47.21 times more likely that there is a difference between horizontal and lower-
 238 right/upper right than that there is none whereas it is only 2.72/2.58 times more likely that
 239 there is a difference between vertical and lower-right/upper right than that there is none. Only
 240 for the comparison between upper-right and lower-right evidence is in favour of the null
 241 hypothesis ($BF_{01} = 3.65$).



242
 243 **Figure 3.** Violin plot of the difference in motion coherence thresholds between conditions (UpR = Upper
 244 right, Hor = Horizontal, Ver = Vertical, LoR = Lower right) with means (red dots) and standard deviations
 245 (red bars).
 246
 247

248 **Table 2.** Multiple comparisons between all conditions presenting t-test results, Bayes factor (BF_{10}) and 95%
 249 bootstrapped confidence intervals (CI).

Comparisons	T-test	BF_{10}	CI
Horizontal – upper right	$t(18) = 4.048, p < 0.001$	47.21	8.66 – 24.76
Horizontal – lower right	$t(18) = 3.423, p = 0.003$	14.23	5.37 – 21.31
Vertical – upper right	$t(18) = 2.506, p = 0.022$	2.58	2.38 – 17.31
Vertical – lower right	$t(18) = 2.474, p = 0.024$	2.72	1.46 – 13.82
Horizontal – vertical	$t(18) = 1.946, p = 0.067$	1.12	1.23 – 16.41
Lower right – upper right	$t(18) = 0.567, p = 0.578$	0.27	-4.9 – 9.19

250

251 *2.3 Discussion*

252 In this Experiment, we determined motion coherence thresholds for coarse motion direction
 253 discrimination for up/down, left/right, upper left/lower right, and upper right/lower left
 254 motion. Our results confirm the oblique effect in motion direction discrimination (Dakin et
 255 al., 2005; Gros et al., 1998). Interestingly, the oblique effect was more pronounced for
 256 horizontal compared to diagonal motion directions than for vertical compared to diagonal
 257 motion directions. In a previous study, we found a significant difference between horizontal
 258 and vertical coarse motion direction discrimination (Pilz et al., 2017). The results from this
 259 study, however, only provide weak evidence for such a difference. In contrast to the present
 260 study, Pilz et al., (2017) only tested vertical and horizontal motion in a larger sample of
 261 participants across two age groups, and it is likely that the difference between the cardinal
 262 conditions was mostly driven by the group of older participants and the absence of the
 263 diagonal conditions. Interestingly, however, Figures 2 and 3 indicate large individual
 264 differences within the group of participants that cannot be explained by general performance
 265 differences. To further investigate these performance differences, in Experiment 2, we
 266 assessed fine motion direction discrimination for cardinal motion directions only. Coarse
 267 motion direction discrimination assesses the ability to discriminate between opposite motion
 268 directions whereas fine motion direction discrimination refers to the ability to discriminate
 269 subtle differences between motion directions. Therefore, results from experiments on fine
 270 motion direction discrimination might allow us to draw conclusions with regards to
 271 differences in the tuning curves of neurons in primary visual cortex tuned to cardinal and
 272 oblique motion directions.

273 Previous studies assessing fine motion direction discrimination across a variety of different
274 directions are scarce and often, performance is assessed based on a small number of highly
275 trained participants. An initial study by Ball and Sekuler (1986) used a same/different task to
276 investigate fine motion direction discrimination for two cardinal and one oblique direction.
277 Overall, performance was better for the cardinal directions, which is in line with Gros et al.,
278 (1998) and Dakin et al., (2005). Fine motion direction discrimination seems to be heavily
279 affected by motion coherence (Pilz et al., 2017; Gros et al., 1998). To assess the effect of
280 motion coherence on fine motion direction discrimination we used predefined levels of 30%,
281 40%, 50%, 60% and 70% motion coherence in a between-subject design.

282

283 **3. Experiment 2**

284

285 *3.1 Methods*

286

287 3.1.1 Participants

288 Seventy-seven young adults (18-33 years, $M = 21.08$, 29 males) participated in the
289 experiment. The same criteria as for the above experiment were applied. All participants were
290 students of the University of Aberdeen and received either two credit points for their
291 participation as part of their curriculum or 6£ reimbursement for their time.

292

293 3.1.2 Apparatus

294 The same apparatus was used as described in Experiment 1.

295

296 3.1.3 Stimuli

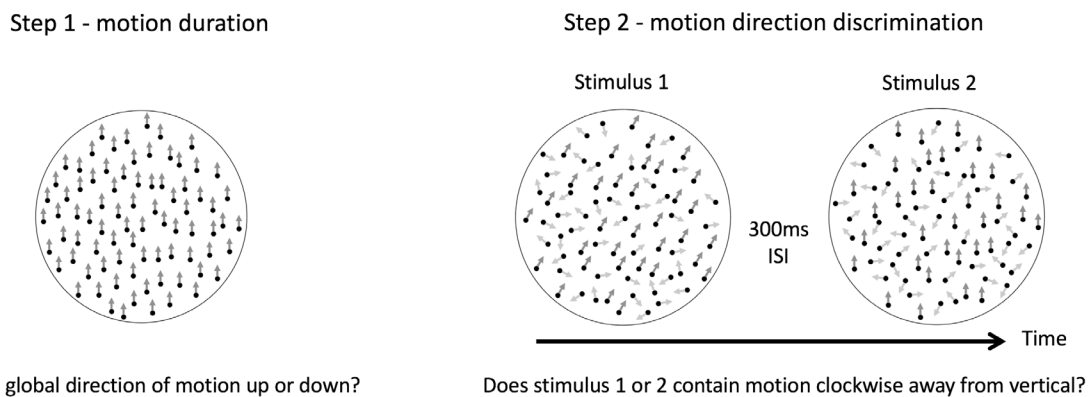
297 Stimuli were similar to the ones used in the previous experiment with the following
298 differences: the random-dot kinematograms (RDKs) contained 150 dots with a size of 2
299 pixels, moving at a speed of 6.4/s, and motion coherence was predetermined for all
300 participants at 30%, 40%, 50%, 60% or 70%.

301

302 3.1.4 Procedure

303 In this experiment, we investigated the effect of coherence on fine motion direction
304 discrimination for horizontal and vertical motion. Two RDKs were presented successively,
305 and participants were asked to indicate in which of the two RDKs the dots moved clockwise
306 away from the control direction by pressing *I* if the first interval contained the target motion

307 and 2 if the second interval contained the target motion. In one of the two RDKs, dots moved
 308 either horizontally (right, 0°) or vertically (up, 90°). In the other RDK, dots moved diagonally
 309 clockwise away from the control direction. The interstimulus-interval was set to 300ms.
 310 There were forty trials each for six angular deviations (3°, 6°, 9°, 12°, 24°, and 44°) that were
 311 randomly intermixed. Participants were seated 52 cm away from the screen and their head
 312 position was stabilized using a chin rest. Each participant performed two experimental blocks
 313 of trials, one block for horizontal and one for vertical motion (Figure 4). The order of blocks
 314 was counterbalanced across participants. Each block was preceded by a practice. In contrast
 315 to Experiment 1, coherence was fixed for all participants. Twelve participants performed the
 316 task at 70% coherence, thirteen participants at 60% coherence, eighteen participants each
 317 performed the task at 30% and 50% coherence, and sixteen participants performed the task
 318 at 40% coherence.



319 Is the global direction of motion up or down? Does stimulus 1 or 2 contain motion clockwise away from vertical?
 320 **Figure 4.** Example of stimuli and trial sequences for both steps of the experiment for vertical motion. In step 1,
 321 performance for coarse motion direction discrimination was assessed at a stimulus duration of 400 ms and 100%
 322 motion coherence. Participants had to determine the global direction of motion for one stimulus that appeared
 323 on the screen. In step 2, participants had to indicate which of two stimuli that appeared sequentially on the
 324 screen contained motion clockwise away from target motion (vertical, horizontal)(Figure adapted from Pilz et
 325 al., 2017)

326
 327 The first step was a motion duration task identical to Experiment 1. This step ensured that
 328 participants were able to discriminate motion at the given stimulus duration and provided
 329 them with some training with regards to the stimulus. The second step was a motion direction
 330 discrimination task using a two- alternative forced-choice paradigm. Before each block,
 331 participants performed 20 practice trials for the given motion direction with 70% motion
 332 coherence and an angular difference of 45° between control and test stimulus. Trial-based
 333 feedback was provided only in the first step and the practice of step 2. Participants who
 334 performed below 60% accuracy in both conditions across all angular deviations during the

335 main experiment were excluded from the analysis. Overall, seventeen out of seventy-seven
336 participants were excluded from the analysis, resulting in a total sample of 60 participants.
337 More specifically, seven participants were unable to perform the task at 30% coherence, two
338 at 40%, five at 50%, two at 60% and one at 70%, which resulted in samples of eleven
339 participants at 30%, fourteen at 40%, thirteen at 50%, eleven at 60% and eleven at 70%
340 motion coherence.

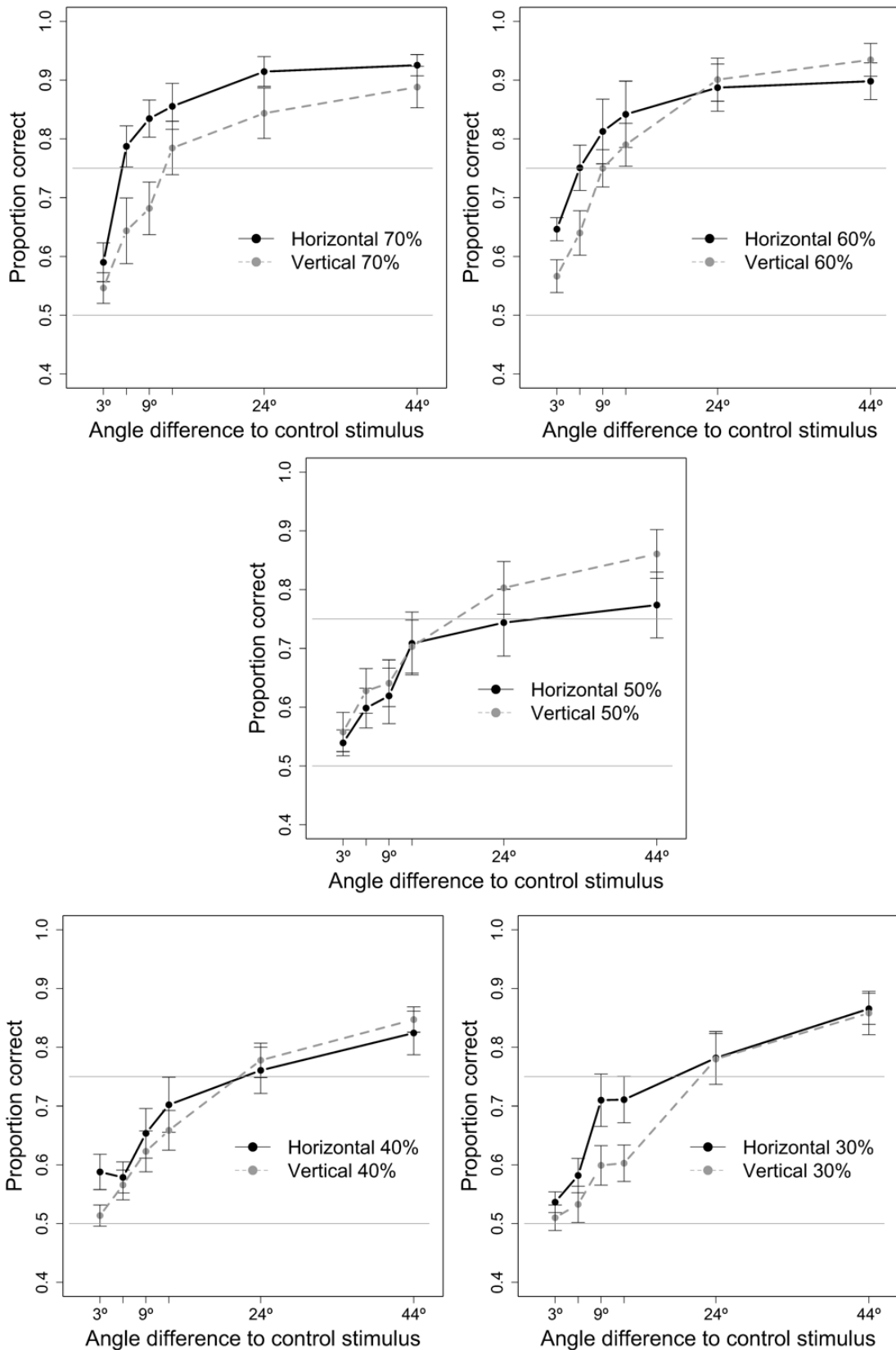
341

342 *3.2 Results*

343 Data were analysed using RStudio (RStudio Team, 2016) and JASP (JASP Team, 2019). To
344 assess the whole range of effects across all tested coherence levels, we performed a mixed
345 design 5(coherence) x 2 (direction) x 6(angle) ANOVA on arcsine transformed data (Figure
346 5). The analysis revealed main effects of motion direction, angle and coherence (Table 3).
347 Interactions were found between motion direction and angle (Figure 6) and angle and
348 coherence. The interaction between direction and coherence (Figure 6), and the three-way
349 interaction between direction, coherence and angle were not significant. In addition to
350 common statistical methods, we also conducted a Bayesian mixed-design ANOVA.
351 Comparing models containing the effect to equivalent models stripped of the effect, we found
352 decisive evidence in favour of the models including the main effect of angle ($BF_{10} > 100$,
353 Table 3) and strong evidence in favour of the model including the main effects of coherence
354 and motion direction ($BF_{10} > 30$). Further, there was decisive evidence in favour of the
355 interaction between motion direction and coherence and strong evidence in favour of the
356 interaction between motion direction and angle. Figure 7 highlights the large variability in
357 performance, in particular with regards to 50% coherence.

358

359



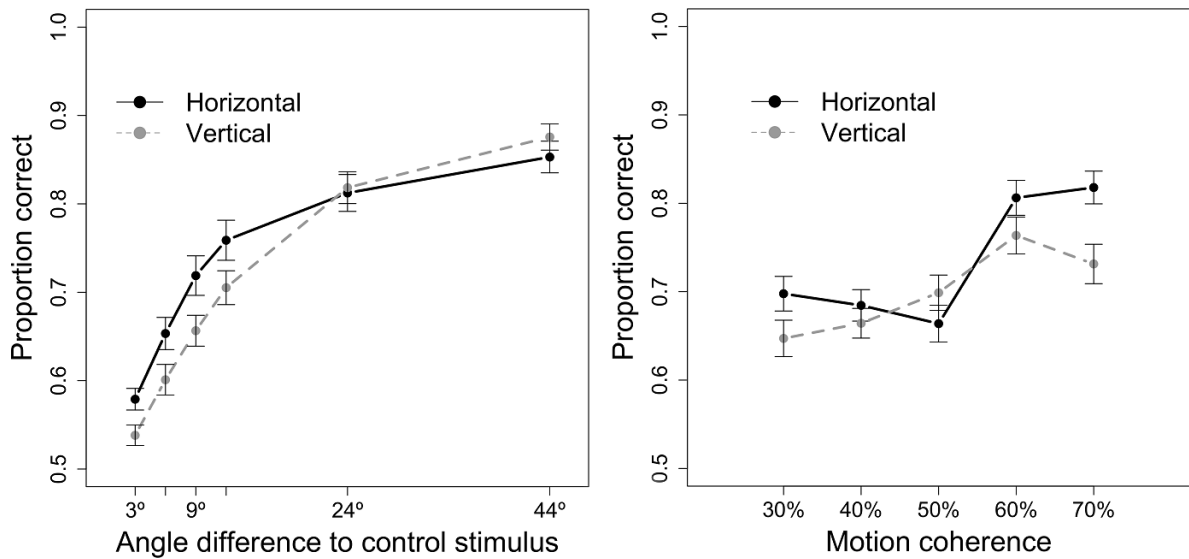
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Figure 5: Direction discrimination performance for horizontal (black) and vertical (light grey) for 70% (upper left), 60% (upper right), 50% (middle), 40% (lower left) and 30% (lower right) coherences. Thin light gray lines indicate 0.75 and 0.5 proportion correct to facilitate comparison between plots. Error bars represent standard errors from the mean.

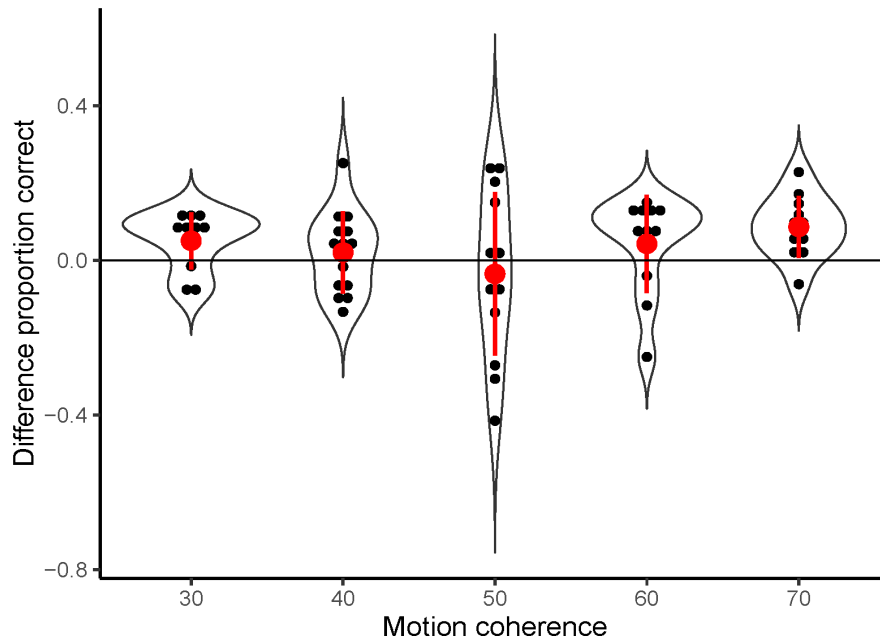
365 Table 3. Results for a standard mixed-design ANOVA (F-value and p-value), effect sizes (η_p^2) and a Bayesian
 366 mixed-design ANOVA ($BF_{inclusion}$).

Effects	F-value	η_p^2	$BF_{inclusion}$
motion direction	F(1, 55) = 3.8, p = 0.055	0.065	58.92
coherence	F(4, 55) = 6.13, p < 0.05*	0.3	70.84
angle	F(5, 275) = 168.91, p < 0.001**	0.75	1.74 * 10 ⁹¹
motion direction x angle	F(5, 275) = 6.187, p < 0.001**	0.1	2.54
motion direction x coherence	F(4, 55) = 1.38, p = 0.25	0.09	161.71
angle x coherence	F(20, 275) = 1.76, p < 0.05*	0.11	0.056
motion direction x angle x coherence	F(20, 275) = 0.84, p = 0.67	0.06	0.005

367
 368
 369



370
 371 **Figure 6.** Left: interaction between motion direction and angle. Direction discrimination performance for
 372 horizontal (dark grey) and vertical (light grey) motion collapsed across coherences. Differences between motion
 373 directions are significant at 3°, 6°, 9° & 12°. Right: interaction between coherences and directions. Direction
 374 discrimination performance collapsed across angular difference between control and test stimulus. The
 375 interaction between coherence and motion direction is not significant.
 376



377
 378 **Figure 7:** Violin plot highlighting the large variability in performance within and between groups with means
 379 (red dots) and standard deviations (red bars). Each dot represents one participant plotted as the difference in
 380 performance between horizontal and vertical for all coherences. Dots above the zero line indicate better
 381 performance for horizontal and dots below zero indicate better performance for vertical.

382
 383 *3.3 Discussion*

384
 385 In Experiment 2, we tested participants on horizontal and vertical fine motion direction
 386 discrimination using predefined motion coherence of 30%, 40%, 50%, 60% and 70%.
 387 Participants were better at discriminating motion away from horizontal than away from
 388 vertical, an advantage that was most pronounced at small angular deviations between target
 389 and test stimulus. These effects are supported by common and Bayesian analyses.
 390 Interestingly, Figures 5 and 6 indicate that a horizontal advantage is strongest at 30% and
 391 70% motion coherence whereas there is a large variability in performance at 50%. The
 392 interaction between coherence and motion direction was not significant using standard
 393 statistical methods. However, using Bayesian statistics, evidence for a model containing the
 394 interaction compared to equivalent models stripped of the effect was strong. Individual data
 395 plotted in Figure 7 also highlights that most participants show an advantage in performance
 396 for horizontal motion for 30% and 70% coherence, whereas there is a large variability in
 397 performance for 50%. It is possible that participants have difficulties discriminating target
 398 from background motion at 50% coherence, an effect that has been observed in previous
 399 studies for contrast (Andersen, Müller, & Martinovic, 2012). However, given the between-

400 subject design, it is also possible that effects are related to between-group differences
401 unrelated to coherence, which needs to be addressed in future studies. To our knowledge, no
402 other study has so far examined the differences in performance between horizontal and
403 vertical motion direction discrimination across coherence levels with a large sample of
404 participants. Gros et al., (1998) assessed performance across different coherence levels and
405 found an increase in performance with an increase in coherence thresholds. However, they
406 did not assess a potential interaction between motion direction and motion coherence.
407 Overall, the results show an increased performance for horizontal fine motion direction
408 discrimination compared to vertical fine motion direction discrimination, an advantage that
409 seems to depend on motion coherence. We will further discuss this phenomenon in the
410 following section.

411

412 **4. General Discussion**

413 In two experiments, we investigated performance for coarse and fine motion direction
414 discrimination. In Experiment 1, we assessed individual motion coherence thresholds for
415 horizontal, vertical, upper right and lower right coarse motion direction discrimination.
416 Overall, an oblique effect was found for motion coherence thresholds for coarse motion
417 direction discrimination: performance was better for cardinal motion directions compared to
418 oblique ones. Even though, the oblique effect was more pronounced between horizontal and
419 diagonal motion directions than vertical and diagonal ones, a difference between horizontal
420 and vertical motion direction discrimination, as described in a previous paper (Pilz et al.,
421 2017), was not significant. It is possible that the group of older adults included in the previous
422 paper drove the effect. Experiment 2 investigated possible differences between horizontal
423 and vertical fine motion direction discrimination with predefined motion coherences. Results
424 support a horizontal advantage, which is particularly pronounced at small angular deviations
425 between control and test stimulus and seems to depend on motion coherence. It is possible
426 that previous studies did not report differences between horizontal and vertical motion
427 direction discrimination, because those are generally smaller and more difficult to assess in
428 small high-performing groups of young participants than differences between cardinal and
429 diagonal axes of motion (Andrews & Schluppeck, 2000; Dakin et al., 2005; Gros et al., 1998).
430 The oblique effect in orientation discrimination has been well-studied (Appelle, 1972;
431 Furmanski & Engel, 2000; Heeley et al., 1997; Nasr & Tootell, 2012; Orban et al., 1984),
432 and it is thought that is based on a prevalence of cardinal contours in our visual environment
433 (Annis & Frost, 1973; Coppola et al., 1998; Girshick et al., 2011). It has also been found that

434 more neurons are tuned to cardinal compared to oblique orientations (Li, Peterson, &
435 Freeman, 2003), and early visual areas show increased responses to cardinal orientations
436 (Furmanski & Engel, 2000). Those studies provide a reasonable approach to understanding
437 the neural mechanisms underlying the oblique effect. It is thought that similar mechanisms
438 provide the basis for the oblique effect in both orientation and motion direction
439 discrimination (Dakin et al., 2005). However, as already mentioned above, studies assessing
440 the neural mechanisms related to the oblique effect in motion perception are relatively sparse.
441 In addition to differences between cardinal and oblique orientations, also a performance
442 difference between the two cardinal orientations has been described. Interestingly, however,
443 the so called ‘horizontal effect’ shows the opposite from the results described in this paper –
444 better performance for oblique and vertical compared to horizontal orientations for high-
445 contrast stimuli presented in noise (Essock, DeFord, Hansen, & Sinai, 2003; Hansen &
446 Essock, 2004; Maloney & Clifford, 2015; Wilson, Loffler, Wilkinson, & Thistlethwaite,
447 2001). The horizontal effect seems to contradict previous studies on the oblique effect. In
448 particular, an evolutionary explanation of the horizontal effect supports that the visual system
449 suppresses the stimuli that are oriented in the most common meridians in the environment,
450 i.e. horizontal, in order for new and information to become more salient. However, it is
451 argued that both effects are based on similar mechanisms – an overrepresentation of
452 horizontal contours in the visual environment. But whereas performance increases for simple
453 horizontal line or grating stimuli, a mechanism that compensates for the overrepresentation
454 of horizontal contours in our visual environment takes effect when such stimuli are presented
455 in noise (Essock et al., 2003; Hansen & Essock, 2004). The horizontal effect, to our
456 knowledge, has not been described for motion stimuli. Therefore, it is difficult to directly
457 relate our results to this effect. Interestingly, however, most behavioural studies on the
458 horizontal effect use detection rather than discrimination tasks, whereas our results and many
459 other prominent studies on the oblique effect for motion or orientation are based on stimulus
460 discrimination. Therefore, it is also possible that the difference between an impairment or
461 enhancement of horizontal orientations and motion directions is based on the differences
462 between the tasks per se: performance in simple detection tasks are often faster and more
463 accurate than discrimination, for which participants have to compare the stimulus properties
464 to those of an internal representation or another simultaneously presented stimulus (Klein,
465 2000; Pilz et al., 2012). It is, for example, possible that at early stages of orientation
466 processing, the visual system compensates for the occurrence of more common visual
467 orientations, whereas at later stages, the processing of common orientations is enhanced.

468 It is difficult to draw more direct conclusions between the horizontal effect in orientation
469 discrimination and our results, and in order to understand whether an enhancement or
470 impairment in processing certain orientations or motion directions reflects specific properties
471 of different stages of processing, future studies are needed.

472 Important to mention at this point is the large variability in performance across both
473 experiments from this paper. Individual differences in performance are often observed when
474 assessing naïve participants in basic visual tasks such as contrast, colour, motion or
475 orientation perception (Billino & Pilz, 2019; Pilz, Zimmermann, Scholz, & Herzog, 2013;
476 Pilz et al., 2017), and extend to visual attention (Pilz et al., 2012) and the processing of visual
477 illusions (Grzeczowski, Clarke, Francis, Mast, & Herzog, 2017). Such heterogeneity
478 suggests that visual perception is highly specific and highlights the importance of considering
479 data from individual participants in addition to commonly used statistical methods.

480 To conclude, our results replicate the oblique effect in coarse motion direction discrimination.
481 More importantly, we find advantages for processing horizontal over vertical motion. Similar
482 to the oblique effect, these results are likely due to a processing hierarchy that is related to
483 the relevance and predominance of certain stimuli in our visual environment. However, future
484 studies are necessary to fully understand the mechanisms underlying the horizontal advantage
485 as described in this study and the large individual differences in performance.

486

487 **Acknowledgements**

488 We would like to thank Cosmin Manulescu, Aureja Balatkaite, Alisa Dambe, Hilary McCall,
489 Sorin Spataru, and Emily Williams for help collecting data for this project. In addition, we
490 would like to thank Sebastiaan Mathôt for helpful discussions with regards to the Bayesian
491 analysis.

492

493 **References**

494 Andersen, S. K., Müller, M. M., & Martinovic, J. (2012). Bottom-up biases in feature-
495 selective attention. *The Journal of Neuroscience : The Official Journal of the Society*
496 *for Neuroscience*, 32(47), 16953–16958. [https://doi.org/10.1523/JNEUROSCI.1767-](https://doi.org/10.1523/JNEUROSCI.1767-12.2012)
497 12.2012

498 Andrews, T. J., & Schluppeck, D. (2000). Ambiguity in the perception of moving stimuli is
499 resolved in favour of the cardinal axes. *Vision Research*, 40(25), 3485–3493.

500 [https://doi.org/10.1016/S0042-6989\(00\)00188-7](https://doi.org/10.1016/S0042-6989(00)00188-7)

501 Annis, R. C., & Frost, B. (1973). Human visual ecology and orientation anisotropies in
502 acuity. *Science*, *182*(4113), 729–731. Retrieved from
503 [http://www.scopus.com/inward/record.url?eid=2-s2.0-](http://www.scopus.com/inward/record.url?eid=2-s2.0-0015900221&partnerID=tZOtx3y1)
504 [0015900221&partnerID=tZOtx3y1](http://www.scopus.com/inward/record.url?eid=2-s2.0-0015900221&partnerID=tZOtx3y1)

505 Appelle, S. (1972). Perception and discrimination as a function of stimulus orientation: the
506 “oblique effect” in man and animals. *Psychological Bulletin*, *78*(4), 266–278.
507 Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/4562947>

508 Barlow, H. B. (1975). Visual experience and cortical development. *Nature*, *258*(5532),
509 199–204. <https://doi.org/10.1038/258199a0>

510 Billino, J., & Pilz, K. S. (2019). Motion perception as a model for perceptual aging. *Journal*
511 *of Vision*.

512 Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of*
513 *Psychology*, *58*, 47–73. <https://doi.org/10.1146/annurev.psych.57.102904.190152>

514 Blakemore, C., & Cooper, G. F. (1970). Development of the Brain depends on the Visual
515 Environment. *Nature*, *228*(5270), 477–478. <https://doi.org/10.1038/228477a0>

516 Brainard, D. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

517 Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance
518 fields: effects of transient covert attention, spatial frequency, eccentricity, task and set
519 size. *Spatial Vision*, *15*(1), 61–75. Retrieved from
520 [http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4332623&tool=pmcentrez](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4332623&tool=pmcentrez&rendertype=abstract)
521 [&rendertype=abstract](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4332623&tool=pmcentrez&rendertype=abstract)

522 Coppola, D. M., Purves, H. R., McCoy, A. N., & Purves, D. (1998). The distribution of
523 oriented contours in the real world. *Proceedings of the National Academy of Sciences*
524 *of the United States of America*, *95*(7), 4002–4006. Retrieved from
525 [http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=19952&tool=pmcentrez&](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=19952&tool=pmcentrez&rendertype=abstract)
526 [rendertype=abstract](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=19952&tool=pmcentrez&rendertype=abstract)

527 Cynader, M., Berman, N., & Hein, A. (1975). Cats raised in a one-directional world:

528 Effects on receptive fields in visual cortex and superior colliculus. *Experimental Brain*
529 *Research*, 22(3), 267–280. <https://doi.org/10.1007/BF00234769>

530 Dakin, S. C., Mareschal, I., & Bex, P. J. (2005). An oblique effect for local motion:
531 psychophysics and natural movie statistics. *Journal of Vision*, 5(10), 878–887.
532 <https://doi.org/10.1167/5.10.9>

533 Daw, N. W., & Wyatt, H. J. (1976). Kittens reared in a unidirectional environment:
534 evidence for a critical period. *The Journal of Physiology*, 257(1), 155–170.
535 <https://doi.org/10.1113/jphysiol.1976.sp011361>

536 Edwards, M., & Badcock, D. R. (1993). Asymmetries in the Sensitivity to Motion in Depth:
537 A Centripetal Bias. *Perception*, 22(9), 1013–1023. <https://doi.org/10.1068/p221013>

538 Edwards, M., & Ibbotson, M. R. (2007). Relative Sensitivities to Large-Field Optic-Flow
539 Patterns Varying in Direction and Speed. *Perception*, 36(1), 113–124.
540 <https://doi.org/10.1068/p5626>

541 Essock, E. A. (1980). The Oblique Effect of Stimulus Identification Considered with
542 Respect to Two Classes of Oblique Effects. *Perception*, 9(1), 37–46.
543 <https://doi.org/10.1068/p090037>

544 Essock, E. A., DeFord, J. K., Hansen, B. C., & Sinai, M. J. (2003). Oblique stimuli are seen
545 best (not worst!) in naturalistic broad-band stimuli: a horizontal effect. *Vision*
546 *Research*, 43(12), 1329–1335. [https://doi.org/10.1016/S0042-6989\(03\)00142-1](https://doi.org/10.1016/S0042-6989(03)00142-1)

547 Fang, L. L., Bauer, J., Held, R., & Gwiazda, J. (1997). The oblique effect in Chinese infants
548 and adults. *Optometry and Vision Science : Official Publication of the American*
549 *Academy of Optometry*, 74(10), 816–821. Retrieved from
550 <http://www.ncbi.nlm.nih.gov/pubmed/9383796>

551 Franconeri, S. L., & Simons, D. J. (2003). Moving and looming stimuli capture attention.
552 *Perception & Psychophysics*, 65(7), 999–1010. Retrieved from
553 <http://www.ncbi.nlm.nih.gov/pubmed/14674628>

554 Furmanski, C. S., & Engel, S. A. (2000). An oblique effect in human primary visual cortex.
555 *Nature Neuroscience*, 3(6), 535–536. <https://doi.org/10.1038/75702>

556 Girshick, A. R., Landy, M. S., & Simoncelli, E. P. (2011). Cardinal rules: visual orientation
557 perception reflects knowledge of environmental statistics. *Nature Neuroscience*, *14*(7),
558 926–932. <https://doi.org/10.1038/nn.2831>

559 Gros, B. L., Blake, R., & Hiris, E. (1998). Anisotropies in visual motion perception: a fresh
560 look. *Journal of the Optical Society of America A*, *15*(8), 2003.
561 <https://doi.org/10.1364/JOSAA.15.002003>

562 Grzeczowski, L., Clarke, A. M., Francis, G., Mast, F. W., & Herzog, M. H. (2017). About
563 individual differences in vision. *Vision Research*, *141*, 282–292.
564 <https://doi.org/10.1016/J.VISRES.2016.10.006>

565 Gwiazda, J., Brill, S., Mohindra, I., & Held, R. (1978). Infant visual acuity and its
566 meridional variation. *Vision Research*, *18*(11), 1557–1564.
567 [https://doi.org/10.1016/0042-6989\(78\)90011-1](https://doi.org/10.1016/0042-6989(78)90011-1)

568 Hansen, B. C., & Essock, E. A. (2004). A horizontal bias in human visual processing of
569 orientation and its correspondence to the structural components of natural scenes.
570 *Journal of Vision*, *4*(12), 1044–1060. <https://doi.org/10.1167/4.12.5>

571 Heeley, D. W., Buchanan-Smith, H. M., Cromwell, J. A., & Wright, J. S. (1997). The
572 oblique effect in orientation acuity. *Vision Research*, *37*(2), 235–242.
573 [https://doi.org/10.1016/S0042-6989\(96\)00097-1](https://doi.org/10.1016/S0042-6989(96)00097-1)

574 Hirsch, H. V., & Spinelli, D. N. (1970). Visual experience modifies distribution of
575 horizontally and vertically oriented receptive fields in cats. *Science (New York, N.Y.)*,
576 *168*(3933), 869–871. <https://doi.org/10.1126/SCIENCE.168.3933.869>

577 Hubel, D. H., & Wiesel, T. N. (1963). Shape and arrangement of columns in cat's striate
578 cortex. *The Journal of Physiology*, *165*, 559–568. Retrieved from
579 <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1359325&tool=pmcentrez>
580 [http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1359325&tool=pmcentrez](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1359325&tool=pmcentrez&rendertype=abstract)
580 &rendertype=abstract

581 JASP Team (2019). JASP (Version 0.9.2).

582 Ke, S. R., Lam, J., Pai, D. K., Spering, M., B., B., JE., R., ... L, T. (2013). Directional
583 Asymmetries in Human Smooth Pursuit Eye Movements. *Investigative Ophthalmology*

584 & *Visual Science*, 54(6), 4409. <https://doi.org/10.1167/iovs.12-11369>

585 Kerr-Gaffney, J. E., Hunt, A. R., & Pilz, K. S. (2016). Local form interference in biological
586 motion perception, 78(5), 1434–1443. <https://doi.org/10.3758/s13414-016-1092-9>

587 Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, 4(4), 138–147.
588 [https://doi.org/10.1016/S1364-6613\(00\)01452-2](https://doi.org/10.1016/S1364-6613(00)01452-2)

589 Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007).
590 What's new in Psychtoolbox-3. In *Perception* 36 (p. 1).

591 Li, B., Peterson, M. R., & Freeman, R. D. (2003). Oblique effect: a neural basis in the
592 visual cortex. *Journal of Neurophysiology*, 90(1), 204–217.
593 <https://doi.org/10.1152/jn.00954.2002>

594 Mackeben, M. (1999). Sustained focal attention and peripheral letter recognition. *Spatial*
595 *Vision*, 12(1), 51–72. <https://doi.org/10.1163/156856899X00030>

596 Maier, J. X., Neuhoff, J. G., Logothetis, N. K., & Ghazanfar, A. A. (2004). Multisensory
597 Integration of Looming Signals by Rhesus Monkeys. *Neuron*, 43(2), 177–181.
598 <https://doi.org/10.1016/J.NEURON.2004.06.027>

599 Maloney, R. T., & Clifford, C. W. G. (2015). Orientation anisotropies in human primary
600 visual cortex depend on contrast. *NeuroImage*, 119, 129–145.
601 <https://doi.org/10.1016/J.NEUROIMAGE.2015.06.034>

602 Miller, L., Agnew, H. C., & Pilz, K. S. Behavioural evidence for distinct mechanisms
603 related to global and biological motion perception. *Vision Research*, 142, 58–64.
604 Retrieved from
605 <https://www.sciencedirect.com/science/article/pii/S0042698917301761>

606 Mitchell, D. E. (1978). Effect of early visual experience on the development of certain
607 perceptual abilities in animals and men. In R. Walk & H. Pick (Eds.), *Perception and*
608 *Experience* (pp. 37–76). New York and London: Plenum Press.

609 Nasr, S., & Tootell, R. B. H. (2012). A Cardinal Orientation Bias in Scene-Selective Visual
610 Cortex. *Journal of Neuroscience*, 32(43). Retrieved from
611 <http://www.jneurosci.org/content/32/43/14921.short>

612 Orban, G. A., Vandebussche, E., & Vogels, R. (1984). Human orientation discrimination
613 tested with long stimuli. *Vision Research*, 24(2), 121–128.
614 [https://doi.org/10.1016/0042-6989\(84\)90097-X](https://doi.org/10.1016/0042-6989(84)90097-X)

615 Pavlova, M. A. (2012). Biological motion processing as a hallmark of social cognition.
616 *Cerebral Cortex (New York, N.Y. : 1991)*, 22(5), 981–995.
617 <https://doi.org/10.1093/cercor/bhr156>

618 Pilz, K. S., Bennett, P. J., & Sekuler, A. B. (2010). Effects of aging on biological motion
619 discrimination. *Vision Research*, 50(2), 211–219.
620 <https://doi.org/10.1016/j.visres.2009.11.014>

621 Pilz, K. S., Miller, L., & Agnew, H. C. (2017). Motion coherence and direction
622 discrimination in healthy aging. *Journal of Vision*, 17(1), 31.
623 <https://doi.org/10.1167/17.1.31>

624 Pilz, K. S., Roggeveen, A. B., Creighton, S. E., Bennett, P. J., & Sekuler, A. B. (2012).
625 How prevalent is object-based attention? *PloS One*, 7(2), e30693.
626 <https://doi.org/10.1371/journal.pone.0030693>

627 Pilz, K. S., Vuong, Q. C., Bühlhoff, H. H., & Thornton, I. M. (2011). Walk this way:
628 approaching bodies can influence the processing of faces. *Cognition*, 118(1), 17–31.
629 <https://doi.org/10.1016/j.cognition.2010.09.004>

630 Pilz, K. S., Zimmermann, C., Scholz, J., & Herzog, M. H. (2013). Long-lasting visual
631 integration of form, motion, and color as revealed by visual masking. *Journal of*
632 *Vision*, 13(10). <https://doi.org/10.1167/13.10.12>

633 Rottach, K. G., Zivotofsky, A. Z., Das, V. E., Averbuch-Heller, L., Discenna, A. O.,
634 Poonyathalang, A., & Leigh, J. R. (1996). Comparison of horizontal, vertical and
635 diagonal smooth pursuit eye movements in normal human subjects. *Vision Research*,
636 36(14), 2189–2195. [https://doi.org/10.1016/0042-6989\(95\)00302-9](https://doi.org/10.1016/0042-6989(95)00302-9)

637 RStudio Team. (2016). RStudio: Integrated Development for R. Boston, MA: RStudio, Inc.
638 Retrieved from <http://www.rstudio.com/>

639 Schiff, W., Banka, L., & de Bordes Galdi, G. (1986). Recognizing people seen in events via

640 dynamic “mug shots”. *The American Journal of Psychology*, 99(2), 219–231.
641 Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/3766815>

642 Sekuler, A. B., Gaspar, C. M., Gold, J. M., & Bennett, P. J. (2004). Inversion Leads to
643 Quantitative, Not Qualitative, Changes in Face Processing. *Current Biology*, 14(5),
644 391–396. <https://doi.org/10.1016/J.CUB.2004.02.028>

645 Takahashi, M., Sakurai, S., & Kanzaki, J. (1978). Horizontal and Vertical Optokinetic
646 Nystagmus in Man. *ORL*, 40(1), 43–52. <https://doi.org/10.1159/000275385>

647 Tanaka, J. W., & Farah, M. J. (1993). Parts and Wholes in Face Recognition. *The Quarterly*
648 *Journal of Experimental Psychology Section A*, 46(2), 225–245.
649 <https://doi.org/10.1080/14640749308401045>

650 Timney, B. N., & Muir, D. W. (1976). Orientation anisotropy: incidence and magnitude in
651 Caucasian and Chinese subjects. *Science (New York, N.Y.)*, 193(4254), 699–701.
652 <https://doi.org/10.1126/SCIENCE.948748>

653 van den Berg, A. V., & Collewijn, H. (1988). Directional asymmetries of human optokinetic
654 nystagmus. *Experimental Brain Research*, 70(3), 597–604. Retrieved from
655 <http://www.ncbi.nlm.nih.gov/pubmed/3384058>

656 Wilson, H. R., Loffler, G., Wilkinson, F., & Thistlethwaite, W. A. (2001). An inverse
657 oblique effect in human vision. *Vision Research*, 41(14), 1749–1753.
658 [https://doi.org/10.1016/S0042-6989\(01\)00089-X](https://doi.org/10.1016/S0042-6989(01)00089-X)

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660