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Pigeons (*Columba livia*) integrate visual motion using the vector average rule: effect of viewing distance

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- 1 Pigeons (*Columba livia*) integrate visual motion using the vector
- 2 average rule: Effect of viewing distance
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13 **Abstract**

14 Integrating local motion signals detected by the primary motion detector is crucial
15 for representing a rigid, two-dimensional motion. The nature of motion integration
16 has been studied using stimuli consisting of two superimposed sinusoidal gratings
17 of different orientations, called plaid motion, and it has been shown that humans
18 perceive integrated motion in the direction where the component constraint lines
19 are intersected. We previously found that pigeons and humans perceive different
20 movement directions from plaid motion; pigeons responded to the vector average
21 direction of the gratings. Although this suggests that the underlying processes of
22 motion integration differ between the two species, the viewing distance in the
23 pigeon experiment, which used a touch panel procedure, was much smaller than in
24 typical human experiments. The current study investigated the potential effect of
25 viewing distance on perception of plaid motion in pigeons. We trained six pigeons to
26 detect whether motion directions were tilted leftward or rightward while a visual
27 display was presented 0 or 40 cm from an operant chamber. The pigeons responded
28 to plaid stimuli for both viewing distance conditions as if they perceived motion in
29 the vector average direction of two-component gratings. The result indicates that
30 the species difference in plaid perception is not an artefact of viewing distance and

31 suggests that pigeons use a different strategy than humans for integrating visual

32 motion.

33 Keywords: visual motion, plaid motion, viewing distance, pigeons

34 Introduction

35 Motion processing is important for visually capable animals as it provides
36 information about prey, predators and conspecifics as well as information about
37 self-motion through optical flow signals. The most basic stage of visual motion
38 processing detects a spatiotemporal change in visual cues (primarily luminance)
39 within local receptive fields (Adelson and Bergen 1985). These 1D motion signals
40 with different preferred locations in the visual field and preferred orientations are
41 then integrated in higher processing stages to represent a rigid 2D motion
42 (Movshon and Newsome 1996). The rule of 1D motion integration across
43 orientations has been explored using plaid motion stimuli (**Figure 1B, C, see also**
44 **Supplementary Movie S1, S2**), in which two gratings drifting in different directions
45 are superimposed (Adelson and Movshon 1982). Due to the aperture problem
46 inherent in the 1D motion detector, 1D motion signals from component gratings are
47 ambiguous in speed and directions; there is a family of possible vectors that lie on
48 the constraint line along the orientation of the grating.

49 Humans perceive integrated 2D motion of plaid in the direction consistent with the
50 intersection of constraint lines (IOC) of components (blue dotted arrows in **Figure**
51 **1B, C**) (Adelson and Movshon 1982). By contrast, at least one avian species,

52 pigeons (*Columba livia*), does not appear to integrate 1D motion components based
53 on the IOC rule (Hataji et al. 2019). Pigeons were presented with a motion
54 stimulus surrounded by numerous pecking keys on a touch monitor, and trained to
55 peck the keys located in the same direction as the motion stimulus. When a plaid
56 stimulus was presented, the pigeons did not respond based on the IOC rule, but
57 pecked the keys positioned at the vector average (VA) of the two components (red
58 solid arrows in **Figure 1B, C**). This result implies that motion integration strategies
59 differ across vertebrate species. This could be due on a proximal level to their
60 neural architectures (Shimizu and Watanabe 2012), ultimately driven by varying
61 ecological requirements (e.g. flying control, Wylie et al. 2018).

62 Behavioral studies of perceptual characteristics in non-human animals (hereafter:
63 “animals”), require consideration of whether the data do reflect the nature of
64 perceptual processing of that animal or the variability of testing methods used
65 across species. In particular, many studies of comparative vision require animals to
66 touch visual stimuli with their nose or beak (for review, Qadri and Cook 2015).

67 Compared to typical psychophysical experiments with humans, this touch panel
68 method results in a large visual angle of the stimulus with the stimulus size
69 enlarged in the visual field; it possibly also induces attentional allocations to local

features. For example, pigeons and bantams (*Gallus gallus domesticus*) perceive the Ebbinghaus illusion in the opposite direction to typical humans (Nakamura et al. 2008, 2014). In humans, the Ebbinghaus illusion was modulated when distant portions of the inducer are erased (Weintraub 1979). Therefore, the birds possibly ignore peripheral parts of the inducer due to their closer viewing distances (but see Nakamura et al. 2008 for analyses controlling visual angle). Furthermore, a recent study showed that a visual size illusion was abolished in bumble bees when the viewing distance was restricted (Howard et al. 2017).

Similar to the Ebbinghaus illusion, humans perceive a plaid motion stimulus in different directions according to the viewing conditions (Yo and Wilson 1992). Although we typically perceive a plaid stimulus moving in the IOC direction, we perceive the VA direction when the stimulus is presented briefly or in a peripheral visual field. Given that humans use VA and IOC solutions to motion integration according to viewing conditions (Bowns and Alais 2006), it is possible that the species difference in motion integration reported by Hataji et al. (2019) was attributable to the difference in viewing distance. Therefore, the present study tested whether the perception of plaid motion in pigeons is affected by viewing distance. Pigeons were trained to classify whether the movement direction of a

stimulus tilted left- or rightward (Goto & Lea, 2003). For training stimuli, we used random dot motion and type 1 plaid motion (where the two component gratings of the plaid move such that the VA and IOC directions are the same) (**Figure 1A, B**). After the pigeons learned the discrimination task, we presented the type 2 plaid, in which VA and IOC directions were dissociated (**Figure 1C**). The training and testing were done using 0 and 40 cm viewing distances. If pigeons responded to a type 2 plaid stimulus in the same manner in both viewing conditions, this would strongly suggest that pigeons integrate visual motion differently than humans.

Methods

Subjects

Six male pigeons participated (mean age: 4.5 years, range: 2-9). They were individually housed and maintained at 80-90% of their free-feeding weights. They had participated in several visual discrimination studies, and three had participated in a motion discrimination study (S2, S3 and S6, Hataji et al. 2019). Water and grit were freely available in the home cage. The experiment adhered to the ethical guidelines of Kyoto University, and was approved by the Animal Experiments Committee of the Graduate School of Letters, Kyoto University (No.

106 18-32).

107

108 *Apparatus*

109 The experiments were conducted in an operant chamber (W/D/H was 41/31/40 cm)
110 (**Figure 2A, B**). A transparent plexiglass occluded the window through which the
111 subjects viewed the visual stimulus on a 15 in. LCD monitor (EIZO, FlexScan
112 L367). The distance between the window and monitor was 0 or 40 cm, depending
113 on the experimental phase. The distance of 40 cm was chosen because pigeons can
114 reliably discriminate the movement direction of grating patterns at that distance
115 (Martinoya and Bloch 1983). The visual angles of the stimulus (119 mm diameter)
116 were 70 and 14° for 0 and 40 cm viewing conditions, respectively, assuming a
117 distance of 85 mm between the bird's head and the window, as obtained from a
118 head tracking study (unpublished data). The space including the chamber window
119 and the monitor was covered with black corrugated plastic boards, preventing the
120 subject from seeing the room in the 40 cm condition. Three response keys with
121 different LED light colors were attached at the top, left and right of the window. A
122 grain hopper delivered food rewards through an opening on the left-side wall. The
123 experiments were controlled by a personal computer (ThirdWave Corporation,

124 Diginnos Series) and a digital input/output module (Contec, DIO-16/16(USB)),
125 running MATLAB with the Psychtoolbox extensions (Brainard 1997).
126 *Stimuli*
127 Random dot motion and type 1 plaid motion were used as training stimuli (**Figure**
128 **1A, B**). The stimulus window was created based on the 2D Gaussian function
129 flattened by the cumulative Gaussian function. The window started to fade around
130 70.1 mm-diameter and alpha value was below 0.1 around 119 mm-diameter. In the
131 stimulus window, white and black dots moved in the same direction on a gray
132 background. The number, size and speed of dots were randomly determined in
133 every trial to prevent discrimination based on potential local features (number: 30
134 – 50, size: 8.9 – 14.9 mm, speed: 35.6 – 142.6 mm/s). The type 1 plaid stimulus was
135 composed of two sinusoidal gratings of different orientations. The spatial
136 frequencies and speeds of both component gratings were the same within a trial,
137 which resulted in the VA and IOC directions being the same. The spatial frequency,
138 speed and relative orientation of the plaid were randomly determined in every trial
139 to prevent discrimination based on potential local features (spatial frequency: 11.9
140 – 29.7 mm/cycle, speed: 35.6 – 142.6 mm/s, relative orientation: 15 – 90°). The
141 direction of dot motion and integrated direction of type 1 plaid was either $\pm 18^\circ$, 54° ,

142 90, 126 or 162° from upward direction.

143 Type 2 plaid motion was used as the probe stimulus (**Figure 1C**). Contrary to the
144 type 1 plaid, the type 2 stimulus plaid was composed of two component gratings of
145 different speeds, which resulted in the VA and IOC directions being different. The
146 speed of one component was twice as fast as the other (35.6 and 71.2 mm/s). The
147 spatial frequencies of the component gratings were 20.8 mm/cycle. The direction of
148 the slower component was either $\pm 18, 54, 90, 126$ or 162° from upward direction.
149 The direction of the faster component was always 30° counterclockwise relative to
150 the slower component, resulting in the VA and IOC directions 20.1 and 66.2°
151 counterclockwise relative to the slower component, respectively.

152

153 *Procedure*

154 The task was to discriminate whether the direction of motion stimulus was
155 orientated left- or rightward (**Figure 2C**). A trial started when the pigeon pecked a
156 self-start key above the window illuminated with white LED. This light turned off
157 and a motion stimulus appeared on the monitor. After 2 sec, two choice keys on the
158 left and right of the window were illuminated by a red and blue LED. The pigeons
159 were differentially reinforced by pecking the keys according to the direction of the

160 stimulus. The left key was correct when the direction of motion stimulus tilted
161 leftward, and vice-versa. Food reward was delivered with a probability of 50%.
162 Regardless of the delivery of the food, the light above the food hopper came on when
163 the subject's response was correct, serving as a secondary reinforcement. This
164 treatment was used to increase the number of trials per daily session. Pecking the
165 wrong key resulted in a 5–7 sec timeout and correction trials were repeated before
166 the next trial until the bird chose the correct key. In a correction trial, the same
167 stimulus appeared, and pecks to the wrong key were not counted in the 5th
168 correction trial. This treatment aimed to prevent response biases. After 3 sec of
169 reinforcement or timeout, the self-start key was illuminated and the next trial (or
170 correction trial) started. The precise duration of access to food varied for each subject,
171 to keep its weight constant. The duration of timeout also varied for each subject:
172 shorter for pigeons who lost motivation and longer for pigeons whose performance
173 did not increase during training.

174 The pigeons were first trained with left- and rightward dot motion ($\pm 90^\circ$) at 0 cm
175 viewing distance. A daily session consisted of 200 trials (2 directions $\times$ 100
176 repetitions). After accuracy of above 80% in one session, four other motion direction
177 conditions were added (± 54 and 126° , each left- and rightward). Another four motion

178 directions were added in the next phase ($\pm 18^\circ$ and 162° , each left- and rightward).

179 After that, a type 1 plaid stimulus was presented on a half of session. The trial order

180 was randomized every session to prevent any order effect. The randomization was

181 conducted for every 20-trial block composed of two stimulus type (dot and plaid) and

182 10 motion directions to prevent the same stimulus type or direction appearing on

183 successive trials. The block-based randomization was repeated 10 times for one

184 session consisting of 200 trials. The pigeons advanced to test sessions if their

185 performances on both dot and type 1 plaid conditions in one session was above 80%.

186 A test session consisted of 180 training and 20 probe trials. All responses in probe

187 trials were reinforced, irrespective of the pigeon's choice. This was done to prevent

188 learning with probe stimuli using cues or criteria other than those in training trials.

189 In a probe trial, the type 2 plaid stimulus was presented. Probe trials were inserted

190 in a semi-randomized way so that they did not appear in two consecutive trials.

191 Between test sessions, at least one training session was conducted to check if

192 performance was above 75%; if not, training sessions were repeated until

193 performance met the criterion.

194 After completing 10 test sessions in which performance on training trials was above

195 70%, training sessions with dot and type 1 plaid stimuli were repeated with the

196 monitor distance gradually increased (10 cm steps). If performance decreased to 70%,
197 the monitor distance was manipulated using smaller steps (3 cm). Then the pigeons
198 advanced to test sessions with the 40 cm monitor distance and completed 10 sessions
199 in which training trial performance was above 70%.

200

201 *Analysis*

202 A modified von Mises distribution, which is a circular distribution analogous to the
203 linear normal distribution, with four free parameters was fitted to the rate of right key
204 responses using least-square minimization with the Matlab function ‘nlinfit.’

$$205 \quad \text{logit}(R(\theta)) = k_1 + k_2 \times \exp(k_3 \times \cos(\theta - k_4))$$

206 The ratio of right key responses $R(\theta)$ was linearized with logit function. The parameter
207 k_1 and k_2 define the upper and lower limits. The parameter k_3 and k_4 define the
208 deviance and peak position. The difference in peak positions between training and
209 probe data was calculated for each individual. To statistically test whether the pigeons’
210 response was consistent with the VA or IOC rule, the deviation of peak position was
211 calculated from the VA and IOC directions. GLMM was fitted to the deviation value
212 with model (VA/IOC) and viewing distance (0/40 cm) as fixed factors and subject ID as
213 a random factor.

214

215 Results

216 All pigeons except for one (S4) completed 10 testing sessions in both viewing
217 conditions. Because S4's performance deteriorated during the test phase at 40 cm, only
218 8 test sessions at this distance were analyzed for this individual. The results are shown
219 in **Figure 3**. **Figure 3A, C** represent the proportion of right key choices and its fitted
220 curve as a function of direction of motion stimulus when the viewing distances were 0
221 and 40 cm, respectively. The pigeons successfully discriminated the direction of dot
222 motion and type 1 plaid at both viewing distances (gray plots). The proportion of right
223 key choices increased as the motion was directed rightward. The response to type 2
224 plaid (black plots) was consistent with the VA rule for both viewing distances. The peak
225 position of right key choice in probe trials shifted 19.7 and 25.6° from baseline for the
226 conditions of 0 and 40 cm viewing distances, respectively. The response to type 2 plaid
227 was plotted as a function of direction of the slower component; hence these shifts were
228 consistent with the VA direction (20.1°) rather than the IOC direction (66.2°). In **Figure**
229 **3B, D** the peak shift and its confidence interval were plotted for each bird at viewing
230 distances of 0 and 40 cm, respectively. The peak shift was placed around the vector
231 average direction for all subjects in both viewing conditions. The deviation of peak from

232 the VA direction was significantly smaller than from the IOC direction ($X^2(1) = 53.777$,
233 $p = 0.000$, $\beta_{std} = 2.542$), and there was no effect of viewing distance (main effect, $X^2(1) =$
234 0.450 , $p = 0.502$, $\beta_{std} = 0.321$, interaction with the VA/IOC model, $X^2(1) = 0.125$, $p =$
235 0.724 , $\beta_{std} = 0.192$), indicating that for both viewing conditions the pigeons responded
236 based on the VA rule.

237

238 Discussion

239 In a study using a touch monitor procedure we previously found that pigeons
240 perceive different motion directions than humans from type 2 plaid stimuli.
241 Whereas humans integrate motion components in plaid based on the IOC rule,
242 pigeons perceive integrated motion based on the VA rule (Hataji et al. 2019). The
243 present study tested whether the species difference merely resulted from different
244 experimental settings because the viewing distance for pigeons was much closer
245 due to the use of touch panel. The present study demonstrated that pigeons
246 responded to plaid stimuli based on the VA rule at both 0 and 40 cm viewing
247 distances. Taken together with the earlier study using a different behavioral
248 procedure (pecking dots surrounding a motion stimulus), this result suggests that
249 pigeons and humans have different motion integration processes.

250 The species difference in visual motion integration could be explained by the
251 difference in the dominant visual pathway and shape of receptive field. Pigeons are
252 known to depend on different visual pathways than primates (Shimizu and
253 Watanabe 2012). Primates depend on the thalamofugal pathway, which relays
254 visual signal from retina to the caudal part of telencephalon through a dorsal part
255 of thalamus, whereas pigeon retinal ganglion cells mainly project to the optic
256 tectum in midbrain. The receptive fields of motion sensitive neurons in optic
257 tectum have different shapes (Jassik-Gerschenfeld and Guichard 1972) compared
258 to visual Wulst, which is evolutionarily homologous to primary visual cortex of
259 mammals (Ng et al. 2010). It is not clear what phylogenetic and ecological factors
260 drive the evolution of the different visual pathways, but the present finding that
261 motion integration processes are different between the two species appears
262 relevant. For example, humans perceived VA direction when the plaid was
263 presented briefly, indicating that VA direction is computed faster than IOC
264 direction (Yo and Wilson 1992). This fast coding of motion information might be
265 crucial for fast flight in pigeons.

266 If the pigeons responded based on VA direction, it is possible that they simply
267 responded probabilistically to both component directions. Another possible

268 confound is that the pigeons responded to the 2D pattern of the plaid and not to
269 visual motion itself, specifically, because the VA direction is almost perpendicular
270 to the checkerboard orientation (see **Figure 1C**). If the pigeons responded to the
271 component direction or 2D pattern, their discrimination performance for type 1
272 plaid should decrease as the difference in component directions increases, because
273 the component directions deviate more from the VA direction and the checkerboard
274 shape changes from rectangle to square. Contrary to this hypothesis, the pigeons
275 performed better as difference in component directions increased (accuracy of 15 –
276 25°, 68.4%; 80 – 90°, 81.7%, $\chi^2(1) = 80.482$, $p = 0.000$, $\beta_{std} = 0.420$, **Supplementary**
277 **Figure S1**), which rules out the possibility that the pigeons responded based on the
278 component direction or checkerboard shape.

279 Humans perceive the plaid motion in the VA direction when it is viewed in the
280 peripheral visual field (Yo and Wilson 1992). This indicates that different visual
281 motion processes work for the fine central and coarse peripheral visions. Pigeons
282 have two areas of retinal density in each eye: the lateral visual field projects onto
283 the central fovea and the frontal visual field projects onto the area dorsalis
284 (Binggeli and Paule 1969; Hayes and Holden 1983). They typically look at close and
285 distant objects with their frontal and lateral visual fields, respectively (Blough

1971), and the velocity threshold and retinal projection are different for frontal and lateral vision (Martinoya et al. 1983; Remy and Güntürkün 1991; Miceli et al. 2006). Therefore, different motion processes might work for the central and lateral vision. In the present study, however, the pigeons looked at motion stimuli with their frontal vision irrespective of viewing conditions. This may be because a 40 cm viewing distance is not enough to induce use of lateral vision, or the pigeons were used to discriminating stimuli with frontal vision due to extensive training using touch panel procedures. Thus, it remains unknown whether the species difference in the perception of plaid motion reflects a difference in motion integration or the visual field where the stimulus is projected. Further studies are needed to address this issue by introducing a procedure to induce the use of lateral vision in pigeons.

297

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302

303 Compliance with ethical standards

304 This study adhered to the ethical guidelines of Kyoto University, and was
305 approved by the Animal Experiments Committee of the Graduate School of Letters,
306 Kyoto University (No. 18-32).

307

308 Competing interests

309 The authors declare no conflicts of interest.

310

311 Data availability

312 The datasets generated or analyzed during the current study and the
313 supplementary stimulus movies and figures are available in the Open Science
314 Framework repository, <https://doi.org/10.17605/OSF.IO/Z4UP3>

315

316 **References**

- 317 Adelson EH, Bergen JR (1985) Spatiotemporal energy models for the perception of
318 motion. *J Opt Soc Am A* 2:284-299. <https://doi.org/10.1364/JOSAA.2.000284>
- 319 Adelson EH, Movshon JA (1982) Phenomenal coherence of moving visual patterns.
320 *Nature* 300:523-525. <https://doi.org/10.1038/300523a0>
- 321 Binggeli RL, Paule WJ (1969) The pigeon retina: quantitative aspects of the optic
322 nerve and ganglion cell layer. *J Comp Neurol* 137:1-18.
323 <https://doi.org/10.1002/cne.901370102>
- 324 Blough PM (1971) The visual acuity of the pigeon for distant targets. *J Exp Anal*
325 *Behav* 15:57-67. <https://doi.org/10.1901/jeab.1971.15-57>
- 326 Bowns L, Alais D (2006) Large shifts in perceived motion direction reveal multiple
327 global motion solutions. *Vision Res* 46:1170-1177.
328 <https://doi.org/10.1016/j.visres.2005.08.029>
- 329 Brainard DH (1997) The psychophysics toolbox. *Spat Vis* 10:433-436.
- 330 Goto K, Lea SE (2003) Discrimination of direction of movements in pigeons
331 following previous experience of motion/static discrimination. *J Exp Anal*
332 *Behav* 80:29-42. <https://doi.org/10.1901/jeab.2003.80-29>
- 333 Hataji Y, Kuroshima H, Fujita K (2019) Pigeons integrate visual motion signals

- 334 differently than humans. *Sci Rep* 9:13441.
- 335 Hayes B, Holden AL (1983) The distribution of displaced ganglion cells in the
- 336 retina of the pigeon. *Exp Brain Res* 49:181-188.
- 337 <https://doi.org/10.1007/BF00238578>
- 338 Howard SR, Avargues-Weber A, Garcia JE, Stuart-Fox D, Dyer AG (2017)
- 339 Perception of contextual size illusions by honeybees in restricted and
- 340 unrestricted viewing conditions. *Proc R Soc B* 284:20172278.
- 341 <https://doi.org/10.1098/rspb.2017.2278>
- 342 Jassik-Gerschenfeld D, Guichard J (1972) Visual receptive fields of single cells in
- 343 the pigeon's optic tectum. *Brain Res* 40:303-317. [https://doi.org/10.1016/0006-](https://doi.org/10.1016/0006-8993(72)90136-9)
- 344 [8993\(72\)90136-9](https://doi.org/10.1016/0006-8993(72)90136-9) (1972).
- 345 Martinoya C, Rivaud S, & Bloch S (1983) Comparing frontal and lateral viewing in
- 346 the pigeon. II. Velocity thresholds for movement discrimination. *Behav Brain*
- 347 *Res* 8:375-385. [https://doi.org/10.1016/0166-4328\(83\)90182-1](https://doi.org/10.1016/0166-4328(83)90182-1)
- 348 Miceli D, Repérant J, Medina M, Volle M, Rio JP (2006) Distribution of ganglion
- 349 cells in the pigeon retina labeled via retrograde transneuronal transport of the
- 350 fluorescent dye rhodamine β -isothiocyanate from the telencephalic visual
- 351 Wulst. *Brain Res* 1098:94-105. <https://doi.org/10.1016/j.brainres.2006.04.091>

- 352 Movshon JA, Newsome WT (1996) Visual response properties of striate cortical
353 neurons projecting to area MT in macaque monkeys. *J Neurosci* 16:7733-7741.
354 <https://doi.org/10.1523/JNEUROSCI.16-23-07733.1996>
- 355 Nakamura N, Watanabe S, Fujita K (2008) Pigeons perceive the Ebbinghaus-
356 Titchener circles as an assimilation illusion. *J Exp Psychol Animal Behav*
357 *Processes* 34:375-387. <http://dx.doi.org/10.1037/0097-7403.34.3.375>
- 358 Nakamura N, Watanabe S, Fujita K (2014) A reversed Ebbinghaus–Titchener
359 illusion in bantams (*Gallus gallus domesticus*). *Anim Cog* 17:471-481.
360 <https://doi.org/10.1007/s10071-013-0679-y>
- 361 Ng BSW, Grabska-Barwińska A, Güntürkün O, Jancke D (2010) Dominant vertical
362 orientation processing without clustered maps: early visual brain dynamics
363 imaged with voltage-sensitive dye in the pigeon visual Wulst. *J Neurosci*
364 30:6713-6725. <https://doi.org/10.1523/JNEUROSCI.4078-09.2010> (2010).
- 365 Qadri MA, Cook RG (2015) Experimental divergences in the visual cognition of
366 birds and mammals. *Comp Cogn Behav Rev* 10:73-105.
367 <https://doi.org/10.3819/ccbr.2015.100004> (2015)
- 368 Remy M, Güntürkün O (1991) Retinal afferents to the tectum opticum and the
369 nucleus opticus principalis thalami in the pigeon. *J Comp Neurol* 305:57-70.

- 370 <https://doi.org/10.1002/cne.903050107>
- 371 Shimizu T, Watanabe S (2012) The avian visual system: overview. In: Lazareva
- 372 OFS, Shimizu T, Wasserman E (ed) How Animals See the World. Oxford
- 373 University Press, Oxford, pp 473–482
- 374 Weintraub DJ (1979) Ebbinghaus illusion: context, contour, and age influence the
- 375 judged size of a circle amidst circles. J Exp Psychol Hum Percept Perform
- 376 5:353–364. <http://dx.doi.org/10.1037/0096-1523.5.2.353>
- 377 Wylie DR, Gutiérrez-Ibáñez C, Gaede AH, Altshuler DL, Iwaniuk AN (2018) Visual-
- 378 cerebellar pathways and their roles in the control of avian flight. Front
- 379 Neurosci 12:223. <https://doi.org/10.3389/fnins.2018.00223>
- 380 Yo C, Wilson HR (1992) Perceived direction of moving two-dimensional patterns
- 381 depends on duration, contrast and eccentricity. Vision Res 32:135-147.
- 382 [https://doi.org/10.1016/0042-6989\(92\)90121-X](https://doi.org/10.1016/0042-6989(92)90121-X)
- 383
- 384

Figure 1 Stimuli used in the present study. (A) White and black dots assigned randomly and moving in a specific direction with 100% coherence and (B) type 1 plaid motion composed of two drifting gratings of the same speed were used for training stimuli. (C) Type 2 plaid motion, composed of gratings of different speeds, corresponding to probe stimuli. Small yellow arrows represent vectors of dot and component grating motion. Red and blue arrows represent the VA and IOC directions, respectively.

Figure 2 Apparatus and procedure. (A, B) The apparatus used in the present study.

A LCD monitor (m) was placed 0 or 40 cm from a transparent window (w) of an

operant chamber. Three response keys (k) were attached on the front wall. A grain

hopper (g) on the left wall delivered food rewards. (C) Schematic illustration of trial

sequence of the motion discrimination task. The pigeons were trained to peck the

left or right key depending on whether the motion direction was tilted left- or

rightward (represented with arrows on the stimulus).

Figure 3 Proportion of right key choice and peak position of fitted function.

(A, C) The proportion of right key choices is plotted as a function of direction of motion stimulus when the viewing distance was 0 (A) and 40 cm (C). For the training data (gray plots), the horizontal axis represents the dot direction and integrated direction of type 1 plaid (L: left, U: up, R: right, D: downward); for the probe data (black plots), it represents the direction of slower component of type 2 plaid. Curved lines and vertical dotted lines represent the fitted function and its peak position. Red and blue lines represent the positions where the peak for probe

413 data should be placed based on the VA and IOC rules, respectively. (B, D) The shift
414 in peak position was calculated from the difference in peak positions between
415 training (gray dotted line in A, C) and probe conditions (black dotted line in A, C).
416 Error bars represent bootstrapped 95% confidence intervals. Red and blue dotted
417 lines represent the VA and IOC directions, respectively.
418