

1 Pigeons (*Columba livia*) integrate visual motion using the vector

2 average rule: Effect of viewing distance

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Abstract

Integrating local motion signals detected by the primary motion detector is crucial for representing a rigid, two-dimensional motion. The nature of motion integration has been studied using stimuli consisting of two superimposed sinusoidal gratings of different orientations, called plaid motion, and it has been shown that humans perceive integrated motion in the direction where the component constraint lines are intersected. We previously found that pigeons and humans perceive different movement directions from plaid motion; pigeons responded to the vector average direction of the gratings. Although this suggests that the underlying processes of motion integration differ between the two species, the viewing distance in the pigeon experiment, which used a touch panel procedure, was much smaller than in typical human experiments. The current study investigated the potential effect of viewing distance on perception of plaid motion in pigeons. We trained six pigeons to detect whether motion directions were tilted leftward or rightward while a visual display was presented 0 or 40 cm from an operant chamber. The pigeons responded to plaid stimuli for both viewing distance conditions as if they perceived motion in the vector average direction of two-component gratings. The result indicates that 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

Introduction

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

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

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

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

Compared to typical psychophysical experiments with humans, this touch panel method results in a large visual angle of the stimulus with the stimulus size 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.

18-32).

Apparatus

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

Diginnos Series) and a digital input/output module (Contec, DIO-16/16(USB)),
running MATLAB with the Psychtoolbox extensions (Brainard 1997).

Stimuli

Random dot motion and type 1 plaid motion were used as training stimuli (**Figure 1A, B**). The stimulus window was created based on the 2D Gaussian function flattened by the cumulative Gaussian function. The window started to fade around 70.1 mm-diameter and alpha value was below 0.1 around 119 mm-diameter. In the stimulus window, white and black dots moved in the same direction on a gray background. The number, size and speed of dots were randomly determined in every trial to prevent discrimination based on potential local features (number: 30 – 50, size: 8.9 – 14.9 mm, speed: 35.6 – 142.6 mm/s). The type 1 plaid stimulus was composed of two sinusoidal gratings of different orientations. The spatial frequencies and speeds of both component gratings were the same within a trial, which resulted in the VA and IOC directions being the same. The spatial frequency, speed and relative orientation of the plaid were randomly determined in every trial to prevent discrimination based on potential local features (spatial frequency: 11.9 – 29.7 mm/cycle, speed: 35.6 – 142.6 mm/s, relative orientation: 15 – 90°). The direction of dot motion and integrated direction of type 1 plaid was either $\pm 18^\circ$, 54° ,

90, 126 or 162° from upward direction.

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

Procedure

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

performance met the criterion.

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

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

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

Analysis

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

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

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

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

Discussion

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

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

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

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Compliance with ethical standards

This study 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. 18-32).

Competing interests

The authors declare no conflicts of interest.

Data availability

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

References

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

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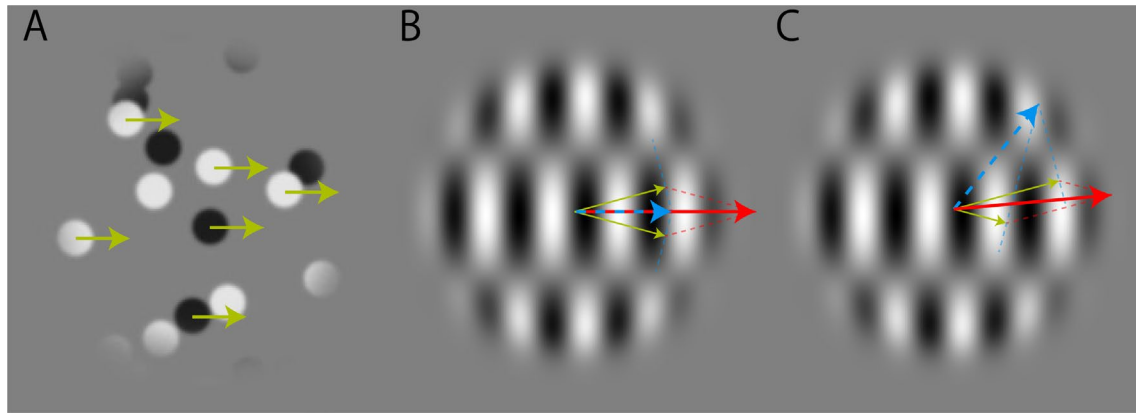


Figure 1 Stimuli used in the present study. (A) White and black dots assigned randomly and moving in a specific direction with 100% coherence and (B) type 1 plaid motion composed of two drifting gratings of the same speed were used for training stimuli. (C) Type 2 plaid motion, composed of gratings of 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.

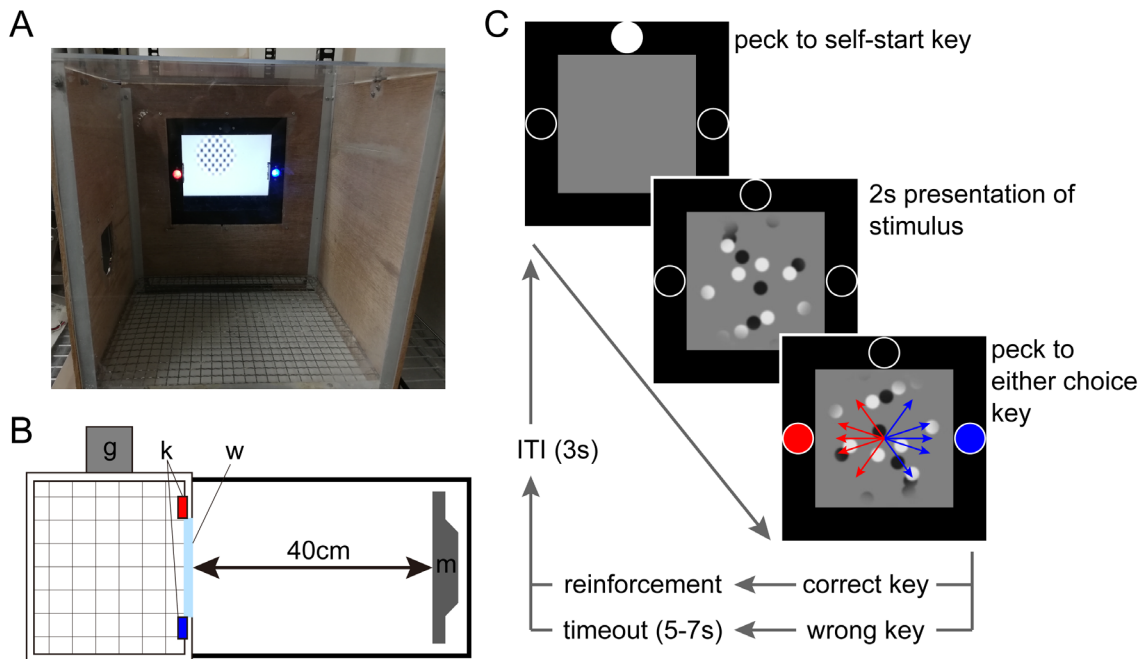


Figure 2 Apparatus and procedure. (A, B) The apparatus used in the present study.

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).

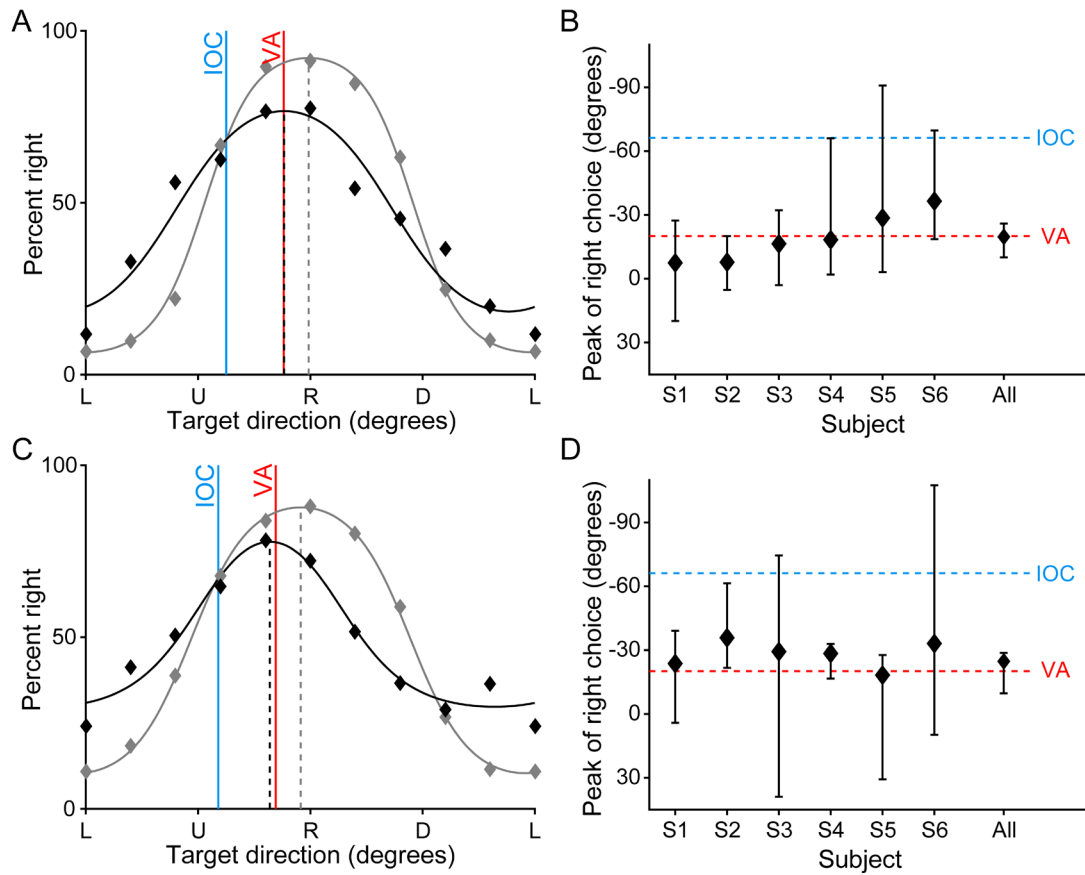


Figure 3 Proportion of right key choice and peak position of fitted function.

(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