

Rapid adjustment of pecking trajectory to prism-induced visual shifts in crows as compared to pigeons.

Hiroshi Matsui^{1 2#}, Ei-Ichi Izawa^{1#}

1 Department of Psychology, Keio University, Tokyo, Japan

2 Japan Society of Promotion for Science, Tokyo, Japan

#Correspondence to:

Hiroshi Matsui

Address: 2-15-45 Mita, Minato-ku, Tokyo 108-8345, Japan

TEL: +81-3-5443-3896

E-mail: hiroshi1004keio.university@gmail.com

Ei-Ichi Izawa

Address: 2-15-45 Mita, Minato-ku, Tokyo 108-8345, Japan

TEL: +81-3-5418-6400

E-mail: izawa@flet.keio.ac.jp

Summary statement:

The visuomotor control of avian pecking is poorly understood. The role of vision was investigated in the pecking adjustments of pigeons and crows to the visual distortion caused by prisms. We found that vision plays a role only before movement initiation in pigeons, whereas crows may use vision during movement.

ABSTRACT

Pecking in birds is analogous to reaching and grasping movements in primates. Earlier studies on visuomotor control in birds, which were conducted mostly in pigeons, suggested that avian pecking is controlled feedforwardly, and is out of the control of visual guidance during movement. However, recent studies using crows suggested a role of vision in pecking control during movement. To unveil what visuomotor mechanisms underlie the flexibility of pecking in crows, the current study examined whether pigeons and crows adjust their pecking to the visual distortion induced by prisms. Because prisms induce visual shifts of object positions, birds were required to adjust their movements. Pecking kinematics were examined before and after attaching prisms in front of the birds' eyes. Analysis of lateral deviation caused by the prisms showed that crows rapidly adjusted their pecking trajectories, but pigeons did slowly. Angular displacement also increased in pigeons after attachment of the prism but decreased in crows. These responses to prisms were consistent among individuals in pigeons but varied in crows, though the adjustment of pecking commonly succeeded in crows. These results suggest that pecking in pigeons predominantly involves feedforward control and that the movement is determined depending on the visual information available before the initiation of pecking. In contrast, the results from crows suggest that their pecking trajectories are corrected during the movement, supporting on-line visual control. Our findings were the first evidence to suggest the on-line visual control of pecking in birds.

Keywords: pecking, crows, pigeons, reaching, grasping, motor control

INTRODUCTION

Pecking behaviour is the fundamental motor repertoire in avian foraging, which is analogous to the reaching and grasping movement in primates, and consists of two motor components, head-reaching and bill-grasping (Bermejo et al., 1989; Delius, 1985). Despite the superficial similarities of these motor actions to primates' arm-reaching and hand-grasping (Delius, 1985; Klein et al., 1985), it is still unknown whether avian pecking is controlled by similar visuomotor mechanisms, because of the clear anatomical differences between primates and birds. In primates, hands and arms (i.e. effector organs) are anatomically separated from the eyes on the head. This body structure enables primate eyes to see the locations of a target and their hands in a stable view, and to control the reaching movement using on-line visual feedback (Keele, 1968; Sarlegna and Mutha, 2015). From a comparative perspective, this primate-type body anatomy with eye–hand/arm separation seems rare in the animal kingdom (e.g. chameleons, frogs, octopus, and praying mantis) and might even be computationally demanding for the transformation of eye and hand/arm coordinates.

Contrastingly, in birds, both the bill and eyes are mounted together on the head, which causes moving the eyes associated with the head-reaching movement. Such body anatomy of birds as associated with eye–head/neck movement coupling seems rather common in both vertebrates and invertebrates, compared to primate-type body anatomy. This avian anatomy raises the question, what visuomotor mechanism controls avian pecking? Specifically, to what extent do birds use vision as a source of information to achieve accurate movements? Given the visual control ability underpinning flight in avian taxa, the visual information generated by the head movement (i.e. optic flow) is likely to be utilised for the control of pecking behaviour.

Previous studies on avian pecking have mostly used pigeons (*Columba livia*) (Bout and Zeigler, 1994; Delius, 1985; Klein et al., 1985, LaMon and Zeigler, 1984; Theunissen et al., 2017; Zweers, 1982), and revealed the capability of visual control in their pecking. Pecking of pigeons consisted of three movement phases: a brief standstill of head movement in front of a target food item (which is called 'fixation'), initiation of head-reaching to the target, and grasping of the target by the bill (Delius, 1985). Once head-reaching has been initiated, pigeons typically close their eyes during pecking, suggesting that vision plays a role only in planning the reaching and grasping movements based on the target location and size determined during fixation, and vision is not involved after initiating the movement (LaMon and Zeigler, 1984). Thus, pigeon pecking is possibly controlled in a feedforward manner, according to movements pre-planned during fixation, and performed without visual movement correction (Goodale, 1983; Theunissen et al., 2017). However, the non-involvement of vision in movement correction during pecking in pigeons was suggested only based on observations by high-speed cinematography. Moreover, the observation in our

previous study suggested that the closing of the eyes during pecking was not necessarily clear in pigeons (Matsui and Izawa, 2017). Thus, the experimental test is necessary to elucidate the role of vision during pecking in pigeons.

In contrast, we recently suggested the on-line visual control of pecking in crows, an omnivorous/carnivorous species (Matsui and Izawa, 2017). Unlike pigeons, based on the observation of video-recorded data, crows opened the eyes during pecking, supporting the possibility of an active role of vision in movement correction during pecking. The on-line visual control of pecking was also suggested by comparing the effects of attaching artificial extensions to their bills on the motor learning of large-billed crows (*Corvus macrorhynchos*) and pigeons. Because the bill extensions distorted the timing of contact to a food, birds were required to adjust their grasping timing to successfully grasp food items. The experiment yielded distinct results between crows and pigeons: crows rapidly adapted to the bill extensions within a few trials, whereas pigeons did not. The rapid learning of successful pecking with the bill extension suggested that the pecking of crows might be under on-line control based on vision. However, there has been no behavioural evidence of the involvement of vision during pecking in birds such as crows.

The purpose of the current study was to comparatively investigate the involvement of vision during pecking between crows and pigeons. Specifically, the involvement of vision was examined using prism-induced visual shifts. Because prism glasses laterally shifted visual images on the retina, subjects were required to adjust their movement in the opposite direction of the visual distortion (Rossi, 1968; 1969; 1971). Based on previous studies (LaMon and Zeigler, 1984) and our findings (Matsui & Izawa, 2017), we hypothesized that the pecking of pigeons would predominantly involve the feedforward mechanism in which the role of vision is limited to before movement initiation. In contrast, we hypothesized that pecking in crows would be under on-line control where vision plays an active role during movements.

Given these hypotheses, specific predictions can be made regarding the different effects of prisms on the pecking movements of pigeons and crows. If feedforward motor control is predominantly involved in pecking, the movement velocity and orientation should be determined depending on the visual information (i.e. the target position on the retina) at the initiation of pecking and cannot be corrected on the basis of visual information until pecking completion. Thus, we predicted that, in pigeons, pecking trajectory would be deviated laterally in response to the prism-induced shift of the target position on the retina at the initiation of pecking. In addition, the correction of the deviated trajectory would occur not quickly but slowly through trial and error because the corrective information would not be obtained after pecking completion. In crows, on the other hand, if on-line visuomotor control is at work, we predicted that the correction of the deviated trajectory could be made by

updating the movement to catch the target in the prism-shifted vision, but not to lose it during pecking and/or that this would be managed in a small numbers of trials.

MATERIALS AND METHODS

Subjects and housing

Three adult pigeons (unknown sex, body weight: 290 – 349 g) and three sub-adult large-billed crows (three females, body weight: 510 – 715 g) were used. All birds were experimentally naive and wild-caught in Tokyo, as authorized by the Environmental Bureau of Tokyo Metropolitan Government (Permission #4005). Pigeons and crows were kept in different rooms, and housed individually in stainless steel-mesh home cages (W 35 cm \times D 30 cm \times H 35 cm for pigeons, W 43 cm \times D 60 cm \times H 50 cm for crows) for approximately one month for the experimental period, plus three days for acclimation to the experimental chamber. Conspecific individuals were placed side-by-side to allow them visual and audio-vocal social communication with one another. During the experimental period, crows were regularly transferred into an outdoor aviary (W 1.5 m \times D 2.8 m \times H 1.7 m) for 2 – 3 hours after daily experimental sessions, to allow crows to bathe and have direct social interactions with other conspecifics, although crows were not provided with food in the outdoor aviary. After all the experiments were finished, birds were transferred back to relatively large outdoor aviaries for group housing (W 3 m² \times H 1.5 m for pigeons, 100 m² \times H 3 m for crows), and used for other behavioural studies. Mixed grains with mineral supplements were fed to pigeons as daily diets, and dry foods, cheese, and eggs were fed to crows, respectively. During the experimental period, no food was provided to the pigeons and crows for five hours before the daily experimental session, and sufficient food was provided after the session. Water was freely available in the home cages. The room was maintained at $21 \pm 2^\circ\text{C}$ in a 13 L:11 D cycle, with light onset at 08:00. The experimental and housing protocols adhered to Japanese National Regulations for Animal Welfare, and were approved by the Animal Care and Use Committee of Keio University (no. 14077).

Apparatus

The experiment was conducted in an experimental chamber (W 35 cm \times D 30 cm \times H 35 cm for pigeons, W 68.5 cm \times D 62 cm \times H 180.5 cm for crows; Figure 1a, b). The chamber for crows consisted of a platform table (W 39 cm \times D 19 cm and 10 cm above the floor). Given the different behavioural patterns of pecking under natural feeding situations, food used as pecking targets was presented on the table in different ways to pigeons and crows in each trial. For pigeons, which feed on seeds and grains, typically by sequential pecking, an array of five corn grains was presented at five specific positions in a line with 5 cm intervals on a frontal wall, 13 cm above the floor of the chamber (Figure 1a). The foods were attached

with moderately adhesive tapes, from which pigeons could pick up the foods. For crows, which typically feed by non-sequential single-shot pecking at a target, a small piece of cheese (approx. less than 1 cm sphere) was attached to the tip of a metal wire to lift it 5 cm above the platform table (Figure 1b). The target position was set to facilitate the birds' approach to the target along a horizontal plane, with less vertical movement. These different methods of target food presentation between pigeons and crows might cause different strategies for the localization of pecking between the two species. However, our previous study, which used similar tasks for pigeons and crows as those in this study, showed that pecking completion, characterised by rapid slowdown and closing the bill immediately before contacting a target, was localized at a specific location in a 3D space (Matsui & Izawa, 2017). Thus, we treated the pecking behaviour of pigeons and crows as comparable to investigate their underlying sensorimotor mechanisms in this study. A high-speed camcorder (300 frame-per-second; Gig-E 200, Library Inc., Tokyo, Japan) was located above the chamber (93 cm for pigeons, and 150 cm for crows). Using these experimental settings, we video-recorded the pecking movements of the birds from a horizontal view for the two species for comparison.

Procedures

For both pigeons and crows, the experiments consisted of the following three phases; *control* (normal eyes) phase (1 – 3 sessions), *prism* phase (10 sessions), and *follow-up* phase (1 session). Each daily session consisted of 10 trials for pigeons and 20 trials for crows, which allowed us to record a maximum of 50 pecks from pigeons and 20 pecks from crows in each session. Thus, the total number of trials throughout the experiment was larger for pigeons than for crows. For all experimental phases, the session was terminated when the subjects consumed all foods or did not show responses for five minutes.

Before the control phase began, the subjects were briefly handled to attach the frames of prism glasses to their eyes with medical glue. The frames of glasses were made from dental resin, which had ellipse-like shapes (1.7 and 1.5 cm major and minor axis for pigeons; 2.0 and 1.7 cm for crows; Figure 1c and 1d). The weights of glasses were approximately 2.5 g for pigeons and 3.5 g for crows. As seen in Figure 1c and 1d, although the attached frames blocked some part of the caudal visual field, the lateral and frontal views were retained in both pigeons and crows. The procedure was performed under anaesthesia induced by inhalation of 3% isoflurane (Mylan Inc., Canonsburg, PA, USA). The control phase started at least after 24 hours after birds awoke from the anaesthesia, to allow the birds to recover from the procedure.

In the control phase, the subjects pecked at the foods without having the prisms attached to their glass frames. The control phase was performed for 1 – 3 sessions, until 50 instances of pecking were recorded for both pigeons and crows. The prism phase started the day after the control phase was completed. The filmy-thin prism (15-diopter; Fresnel prism, 3M

company, MN, USA) was attached to the glass frames just before the prism session was begun. Anaesthesia was not used during prism attachment because the procedure was not considered to be painful, and took less than five minutes to complete. The prism was attached so as to shift the perceived position of foods 8.5 degrees to the right, and remained attached after the daily experimental sessions. Thus, the subjects were involved in additional feeding and other daily activities in their cages whilst wearing prism glasses. Ten prism sessions were performed for each bird. The follow-up control session was conducted one week after the last prism session. Total experimental periods were 20 – 21 days, which included a week-long recovery period between the prism phase and the follow-up phase.

Statistical Analysis

A single pecking movement was extracted from video images. We defined a pecking instance as an initiation-to-completion sequence of movements from the head fixation, which was characterized by a 70 – 90 -msec brief standstill of the head in front of a target food (i.e., F2 as described in Goodale, 1983), to a grasping offset, which was defined as the minimal head-movement velocity at the timing of grasping (Matsui & Izawa, 2017). For the kinematic analysis, horizontal x-y coordinates of tracking markers were extracted using tracking software (Move-tr/2D v. 7.0, Library Inc., Tokyo, Japan). Small pieces of square-cut white tape were attached to the head for pigeons (0.5 cm × 0.5 cm), and to the head and middle of the bill for crows (1 cm × 1 cm), as tracking markers (Figure 1a and 1b). The distance between the two markers was 3 cm and 5 cm for pigeons and crows, respectively. Nose knobs were also used as tracking marker for pigeons. Two tracking-point were video-recorded to extract their coordinates on the horizontal plane. Pecking instances in which tracking points were framed-out or missing by head tilting were removed from the analysis. Although 8.1% (105) of the trials in pigeons and 7.1% (44) of the trials in crows were removed from the analysis, we obtained a sufficient number of instances for the reliable analysis of the effect of laterally shifted vision.

Extracted coordinates were smoothed using the smooth spline function to reconstruct pecking movement trajectory. Specifically, the Butterworth low pass filter with a 3 Hz cut-off frequency was applied to both x-y coordinates to remove noise. To compare different movement trajectories among trials, an ‘ideal line’ for each trajectory was defined as a straight line from the initial bill coordinate to the target coordinate and subsequently, trajectories of different trials were aligned to the ideal line for each phase of each species. Also, to examine the effect of the prism on the entire course of the movement trajectory, the length of each ideal line was normalised as 0 – 100 % distance by segmenting it into 101 points. To analyse for the same duration of pecking movement between pigeons and crows, we used the aligned trajectory data without normalising the distance of the ideal line.

Two analyses were conducted to examine the effects of the prism on pecking movement for the comparison between pigeons and crows. One is the analysis to examine lateral deviations of pecking movement trajectory in response to the visual shift caused by prism attachment. The lateral deviation for each normalised point or actual time point was measured as the distance of the perpendicular line from the bill coordinate (i.e., nose knob for pigeons, and a marker on the bill for crows) onto the ideal line. This measurement of deviation decreases when subjects move closely along the ideal line with their bills facing ahead to the target food, while it increases when subjects move away from the ideal line laterally with their bills tilting to the left/right of the target food. Although the initial head/bill position was not controlled for this experiment, this measurement with the alignment of ideal lines enabled us to compare the deviations among different trajectories, independently of the initial bill positions. Also, it is noted that lateral deviations were not normalised for any analyses because lateral and ideal-line directions were orthogonal, and no effect on the measurement could be produced for each direction.

To examine the deviation of movement trajectory caused by the prism, we compared lateral deviations in the prism and follow-up phases with the control phase by using linear mixed models. For the analysis with normalised ideal-line distance, comparisons of deviations were performed at 10, 30, 50, 70, and 90% points. The linear mixed models included the phases, % points, and the interaction between these explanatory variables, as well as the individual bird as a random effect. If the interaction was significant according to the likelihood ratio test, further model analyses were performed separately for each phase. The differences in deviation at each % point between the control and prism phase were compared using 95% confidence intervals of estimated parameters of the model.

Lateral deviations were also analysed on the actual movement duration. Two analyses were conducted separately for 0.1 seconds after the initiation of pecking and for 0.1 seconds before the completion of pecking (i.e., grasping offset). Deviations during these 0.1-sec durations were analysed at five time points (0.01, 0.0325, 0.055, 0.0775, and 0.1 sec) after pecking initiation, as well as before pecking completion. Similar mixed models to the analysis with normalised distance were applied to these analyses.

In addition, to verify the change of head orientation during the movement, we analysed the angular displacement. An angular displacement was calculated between the two head-bill vectors from two given points. Specifically, we calculated the angular displacements from the initiation of pecking to a given % point or an actual time point. This calculation provides the degree to which the subjects turned their heads from the start of pecking. Similarly to the analysis of lateral deviation, the angular displacement in each prism phase and the follow-up phase were compared with the control phase using linear mixed models. These model analyses were performed on the % points (i.e., normalised ideal-line distance) as well as the initial and final 0.1 seconds. For the analysis of angular displacement, comparisons were

made within the phases, that is, the comparison of the angular displacement from the initiation of pecking to each subsequent % point and actual time point. The differences in angular displacement for these comparisons were determined using the 95% confidence intervals of estimated parameters of the model. Note that angular displacements to the right and left were not separated but merged to elucidate the increase or decrease of the displacement because the left or right shift was proven from the lateral deviation analysis.

All analyses were performed using R statistical software, version 3.4 (R Core Team, 2016). We used the ‘lme4’ package for the generalized linear model (Bates et al., 2015), and the ‘car’ package for the likelihood ratio test (Fox and Weisberg, 2011).

RESULTS

Pigeons

A total of 1,296 instances of pecking were recorded from the three pigeons. This included 150 instances in the control session, 80 in session (S) 1, 192 in S2 – 4, 303 in S5 – 7, 429 in S8 – 10, and 142 in the follow-up session. Success rate of food ingestion significantly decreased from S1 to S5 – 7, and recovered slightly in S8 – 10 (GLMM with a binomial error distribution and a logit link function, $\chi^2 = 123.73$, $df = 5$, $p < 0.001$; Figure 2a). These performances were the same if corrective pecking (i.e., a sequential movement following the first miss pecking) was included, because all 66 corrective-pecking instances in the prism phases resulted in unsuccessful food ingestion (Table S1).

At the level of pecking movement parameters, no significant effects of the prism were clearly found in the movement distance, duration, mean velocity, peak velocity, or relative time of peak velocity (Table 1). These results suggest that pigeons did not change their pecking movement in response to prism attachment at the level of these movement parameters.

Deviation analysis with normalising ideal line distance revealed a significant interaction between the phase and the % point ($\chi^2 = 539.93$, $df = 20$, $p < 0.001$; Figure 3a). Subsequent analyses to compare the deviation at each % point showed significant deviations rightward at the 90, 70, 50% points of S1 and S2 – 4, in comparison to the control, corresponding to the visual shift by the prism. Similar deviations after prism attachment in S1 and S2 – 4 were confirmed by the analysis with the actual movement duration for the initial and the last 0.1 sec of pecking (Figures S1a for the initial 0.1 sec and S2a for the last 0.1 sec). These rightward deviations at the group level were confirmed at the individual level. All three pigeons consistently increased the deviation to the right in S1 and S2 – 4, compared to those of the control of each individual (Figure 4).

Angular displacement analysis with normalising ideal line distance produced significant main effects for the phase ($\chi^2 = 177.46$, $df = 5$, $p < 0.001$) and the % point ($\chi^2 = 3678.79$, $df =$

4, $p < 0.001$), with no significant interaction between them ($\chi^2 = 26.44$, $df = 20$, $p = 0.152$, *ns*; Figure 5a). For the phase variable, a significant difference was found only between the control and S1. For the % point variable, significant differences were found between the control and all the other phases. Similar results were confirmed by the analysis with the actual movement duration for the initial and the last 0.1 sec of pecking (Figures S3a for the initial 0.1 sec and S4a for the last 0.1 sec). At the level of individuals, all three pigeons showed a similar trend of increasing angular displacement particularly in S1 and S2 – 4 (Figure 5). Given the rightward shift by the prism attachment in the deviation analysis, these increases of angular displacement reflect the head/bill tilting to the right after prism attachment.

All of these results from the deviation and the angular displacement consistently indicate that the movement trajectory of pigeons was deviated to the right with an increase of rightward angular displacement correspondingly to the visual shift caused by prism attachment. Deviated trajectories were corrected, not quickly in S1 or S2 – 4, but slowly in the later phases S5 – 7 or S8 – 10.

Crows

A total of 624 instances of pecking were recorded from the three crows. This included 142 instances in the control, 32 in S1, 129 in S2 – 4, 123 in S5 – 7, 140 in S8 – 10, and 58 in the follow-up. The success rate of food ingestion decreased only in S1, but recovered in S2 – 4 and later phases (GLMM with a binomial error distribution and a logit link function, $\chi^2 = 171.1$, $df = 5$, $p < 0.001$; Figure 2b). Corrective pecking was observed particularly in one bird (crow#1), but only in a few instances in the other crows (Table S1). This suggests that the rapid recovery of success rate in crows cannot be due to corrective pecking.

In pecking movement parameters, a significant decrease was found in the mean velocity and the peak velocity after prism attachment in S1, S2 – 4, and S5 – 7, and also in the movement duration in S2 – 4 (Table 1). These results suggest that crows decreased the velocity of pecking movement after prism attachment.

The deviation analysis with normalising ideal-line distance revealed no significant interaction between the phase and the % point ($\chi^2 = 28.05$, $df = 20$, *ns*; Figure 3b). The deviation analysis with the actual movement duration for the initial and the last 0.1 sec of pecking movement produced similar results to those with normalised distance (for details see Figures S1b and S2b). At the individual level, the three crows showed different movement trajectories (Figure 7): Crows #1 and #3 moved towards the target with right-hand curving (Figures 7a and 7c), and crow #2 showed a left-hand curve (Figure 7b). After prism attachment, crow #1 showed large deviations both to the left and the right across the ideal line within S1, S2 – 4, and S5 – 7 phases. Crow #2, changed its movement direction from the left-hand curve to a slightly left-hand curve (almost straight ahead on the ideal line with just a

small deviation), after prism attachment. Crow #3 weakly displayed the rightward deviation in S1 but, in the subsequent phases, showed no clear deviation compared to the control. These results suggest that crows did not show a simple deviation of movement trajectories corresponding to the visual shift to the right caused by the prism but changed their trajectories in different ways between individuals.

Angular displacement analysis with normalising ideal line distance produced a significant interaction between the phase and the % point ($\chi^2 = 47.90$, $df = 20$, $p < 0.001$) with significant main effects for the phase ($\chi^2 = 136.32$, $df = 5$, $p < 0.001$) and the % point ($\chi^2 = 1069.00$, $df = 4$, $p < 0.001$; Figure 4b). Comparisons with the 95% confidence intervals revealed a significant difference between the 10 % and the other points in all the phases. In addition, a significant decrease of displacement was found at the 30% point between the control and S1. Similar decreases of angular displacement in S1 were confirmed by the analysis with the actual movement duration for the initial 0.1 sec (Figures S3b). For the last 0.1 sec, no significant effect of angular displacement was found at any time points of any phases (Figure S4b). At the individual level, the crows changed their angular displacement, but in different ways, immediately after prism attachment (Figure 8). Crow #1 increased the angular displacement in S1 and gradually decreased to the control level in the subsequent phases (Figure 8a). Crows #2 and #3 apparently decreased their angular displacements in S1 and thereafter, compared to the control (Figures 8b and 8c).

The results from lateral deviation and angular displacement suggest that crows commonly exhibited a rapid adjustment of pecking movement in response to the visual shift caused by the prisms, but their responses were different among individuals.

DISCUSSION

The current study aimed to examine the visuomotor controlling mechanisms of pecking in crows and pigeons, using prism-induced visual shifts. We found contrasting results between pigeons and crows: In pigeons, the pecking movement in the control was basically straight ahead with small lateral deviation and angular displacement during pecking. The deviations and angular displacements of pecking in pigeons both increased after prism attachment corresponding to the visual shift caused by the prisms, and were adjusted, not quickly, but slowly to the control trajectory. These effects of prisms, including the success rate of pecking, were consistent among individuals. In crows, on the other hand, the pecking movement in the control was curved to the right or left, differently among individuals or trials of the same individuals, with relatively large deviation and angular displacement during pecking. The deviations and angular displacements of pecking in crows were not changed or even decreased after prism attachment at the group level, and were adjusted quickly to the

control trajectories or even to new ones. Although the effects by prisms were different among individuals or trials of the same individual, the quick adjustment to the visual shift caused by the prisms were consistently achieved in all the crows. These results support the predictions that the pecking of pigeons and crows are primarily under feedforward control and on-line visual control, respectively. Our results provide the first evidence to suggest on-line visuomotor control in pecking of birds.

The effects of prisms on both deviation and angular displacement in pigeons support the traditional view that the pecking mechanism is primarily under feedforward control (Goodale, 1983; LaMon and Zeigler, 1984; Matsui & Izawa, 2017). In pigeons, the lateral deviation and angular displacement of movement trajectories from the initiation to the completion of pecking was small, at around 0.5 cm and 10 degrees, respectively, in the control condition (Figure 3a). These movement parameters reflected the nearly straight, though slightly curved, trajectory of pecking movements in pigeons. Prism attachment increased the rightward deviations until the phases S2 – 4 and angular displacement in S1 (Figures 3a and 5a), indicating that the movement trajectories were shifted to the right, without clear change in shape, correspondingly to the rightward visual shift caused by prism attachment. Such trajectory shifts caused by prisms suggest that the movement trajectory of pecking in pigeons depends highly on the visual information immediately before the initiation of pecking, which supports the feedforward control of pecking. In addition, the deviated trajectories were corrected, not rapidly, but gradually in the subsequent S5 – 7 and S8 – 10 phases (Figure 3a), suggesting that movement correction was made, not during pecking, but after pecking completion, based on peck-by-peck updates. This gradual correction through the phases is also consistent with the feedforward control of pecking in pigeons.

In crows, on the other hand, on-line control is supported by both the deviation and angular displacement analyses. Compared to pigeons, both the lateral deviation and angular displacement of movement trajectories in crows were large and variable between the initiation and the completion of pecking, at around 1.5 cm and 30 degrees, respectively, in the control condition (Figure 3b and 5b). These movement parameters indicated the curved trajectory in crows, which is very different from that in pigeons. The effects of prisms on the pecking movements of crows were also different from those found in pigeons. Crows did not show increased deviations in movement trajectories after prism attachment (Figure 3b). Moreover, angular displacement decreased in S1, soon after prism attachment, which was opposite to the expected effect of the prism-induced visual shift. This decrease of angular displacement, given its minimal effect on lateral deviation, suggests that crows corrected their movement trajectories to be less curved, against the visual shift caused by prism attachment.

These small or brief effects of the prisms on lateral deviations, based on the absence of statistically significant effects, might be caused by the large individual variations of movement trajectories masking the actual effects on each individual movement. However,

this is unlikely. As shown in figures 7 and 8, all three crows moved differently in the control condition but also coped differently with prism attachment. Specifically, crow #1 increased deviations slightly to the right but also to the left, including the switching of left- and right-curved movements among trials, and showed angular displacement after prism attachment until S5 – 7 (Figures 7a and 8a). This crow #1 corrected the deviated trajectories not soon after prism attachment, but gradually through the subsequent phases. These effects on deviation and angular displacement caused by the prism in crow #1 were similar to those in pigeons. In crow #2, the prism caused a rightward shift of deviations (Figure 7b). However, this rightward shift of trajectories could not be the prism-induced deviations because, if the movement was distorted by prism, the position of the target food on the retina would be shifted the right at the final course of the movement (i.e. 70 – 90% points) and the trajectories should pass over the right side of the target. Interestingly, this individual #2 decreased the range of lateral deviation by reducing angular displacement and even displaying no displacement through the course of pecking immediately after prism attachment (Figure 8b), indicating that this crow changed its trajectories to move straight ahead to the target. Crow #3 also reduced angular displacement and successfully reached the target immediately after prism attachment (Figure 7c and 8c). Although there were individual variations in pecking movement in the crows, all three crows commonly showed immediate changes in their pecking trajectories (e.g. decreasing deviation and angular displacement) to cope with the visual shift caused by the prisms. The small or brief effects on pecking movement caused by the prisms at the individual level were consistent with the results from the group level analyses, supporting the involvement of on-line visual control in pecking.

Rapid adjustment of pecking movement in response to the prisms in crows could be facilitated by decreasing the pecking velocity. As we found in the analysis of movement parameters (Table 1), crows showed a slowing down of the mean and the peak velocity immediately after prism attachment (S1) until S5 – 7 (Table 1). This velocity slowdown could increase the degree of freedom, which could facilitate the correction of movement by the crows so as not to lose the target from their prism-shifted vision and to reach the target. In contrast, velocity slowdown was not observed in pigeons, despite no external constraints for pigeons to do so in the current experimental settings (Table 1). This fact also suggests that the pecking of pigeons is a ballistic movement, predominantly under feedforward control, and it is difficult to employ on-line visual control even if it might play a role in other behavioural contexts.

Contrasting results from pigeons and crows cannot be accounted for by the differences in the experimental tasks between the two species. The tasks for pigeons and crows in this study were different in their target presentation and the total amount of pecking experiences. For pigeons, the small grains, as multiple targets, were presented in lines on the wall, whereas one small piece of cheese was presented on a wire tip for the crows. As we described in the

methods section, the pecking movements of pigeons and crows for these differently presented targets is considered to be comparable for the kinematic analysis in our study. However, the target presentation for pigeons might be advantageous to correct for the deviated movement caused by the prisms because overshoot pecking caused by the prisms was externally stopped by the wall as a corrective cue. However, even if crows missed the target because of the prisms, such corrective cues were externally available. The total number of pecking experiences with prism attachment were higher for pigeons (i.e. 50 pecks per session) than for crows (i.e. 20 pecks per session). These differences in the amount of experiences with the prisms might also be more facilitative for the pigeons than the crows. If the present results were accounted for by the differences in these task settings, movement correction against the prisms might be more facilitative to the pigeons than to the crows, but the results were opposite. Thus, the task settings, such as target presentation and the amount of pecking, cannot explain the contrasting results in this study.

Although our present findings support the involvement of on-line visuomotor control mechanism in the pecking of crows, we did not directly determine the role of vision in the control of on-going movement. However, recent studies in carnivorous/omnivorous generalist birds, such as crows, suggest the active role of vision in the control of pecking or neck-reaching-based foraging behaviour. In our previous study, large-billed crows, a non-tool-using species in the wild, were reported to use visual information for experimentally-trained tool manipulation. Specifically, their rake-tool use to retrieve food on a platform table was severely deteriorated by blocking the visual information on the table with an opaque cover (Kanai et al., 2014). New Caledonian crows, a tool-using bird in the wild, were suggested to use vision for their dextrous tool use. This crow species was proved to have extraordinarily large frontal-visual fields (Troschianko et al., 2012), which is assumed to facilitate tool manipulation within the wide frontal view, together with their characteristic up-turned bills (Matsui et al., 2016). It has also been reported that New Caledonian crows used individually-preferred sides of their eyes (i.e. laterality) for tool manipulation (Martinho et al., 2014), although the crows in this study showed movement trajectories from both the left and right sides among the trials within the same individuals without clear lateralisation (Figure 7). All of these recent findings on crows are in good accordance with the present finding of the role of vision in on-going movement control.

In conclusion, our present results on crows provide the first behavioural data to strongly support on-line feedback control in the pecking of birds, beyond the traditional hypothesis of the feedforward control of avian pecking. The traditional feedforward hypothesis of pecking was derived from pigeons, which are ground-feeders (LaMon, & Zeigler, 1984; Delius, 1985). Feedforward motor control is advantageous for ground-feeding forager birds because ballistic pecking enables birds to ingest static and tiny foods (e.g. seeds) rapidly and accurately. In contrast, crows are omnivorous generalists, and capture moving prey species,

so that flexible pecking control during the movement is necessary to capture escaping prey. These differences in foraging ecology between avian species are assumed to drive the different neuromotor control mechanisms of pecking. This provides a novel research direction on visuomotor mechanisms underlying dexterous foraging skills, such as tool use in corvids, and in other carnivorous/omnivorous generalist avian species.

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Competing interests

The authors declare no competing financial interests.

Author Contributions

Conceptualization: H.M, E-I. I.; Methodology: H.M.; Formal Analysis: H.M.; Investigation: H.M.; Writing – original draft: H.M.; Writing – review & editing: H.M., E-I. I.; Project administration: E-I. I.; Funding acquisition: H.M., E-I. I.

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Figures

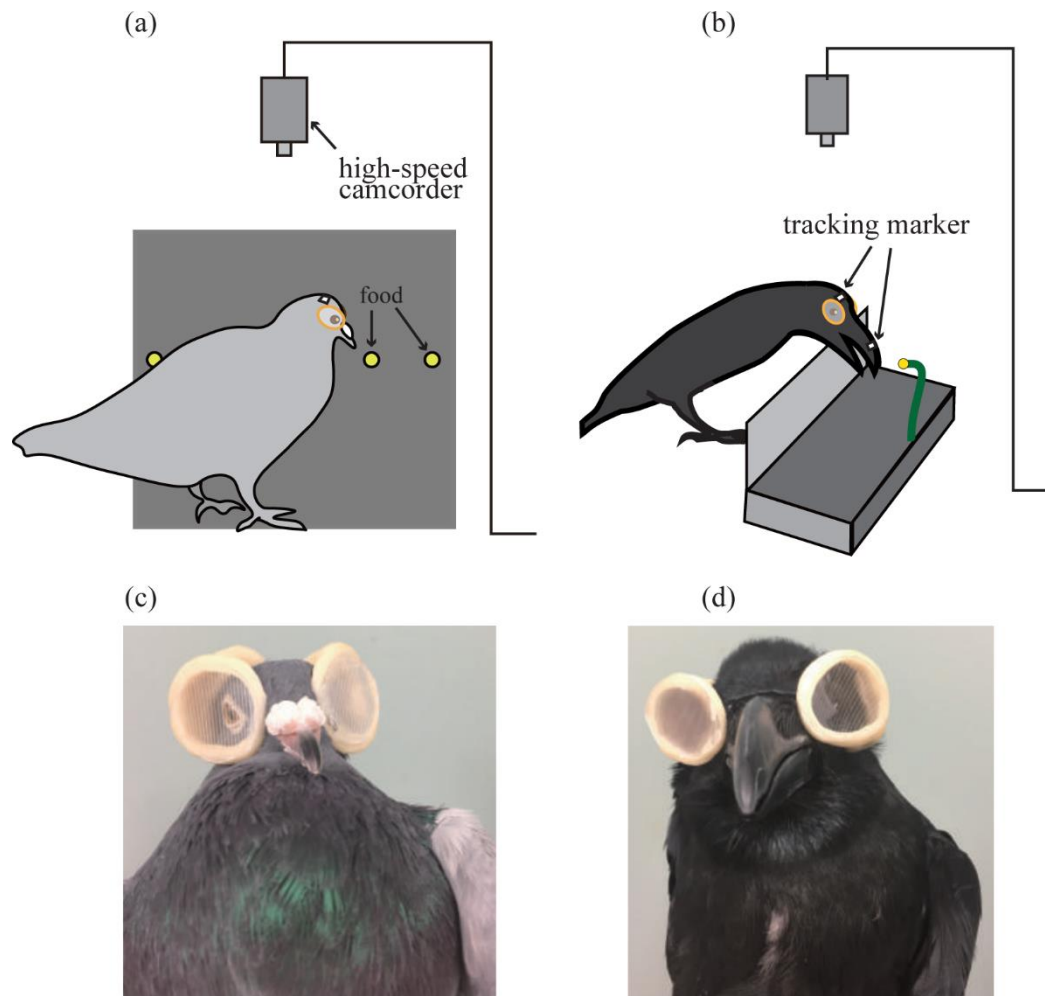


Figure 1. Schematic illustration of the experimental setting. Pecking movements were video-recorded with a high-speed camcorder mounted above the chamber to track horizontal coordinates of tracking markers (square-cut white pieces of tape, depicted in the figure). (a) For pigeons, five food items (corns) were attached to one of the walls of the chamber with adhesive tape. (b) For crows, the experimental setup was slightly different from that of pigeons. A crow pecked at a single food (a piece of cheese), which was attached to a wire on a platform. (c, d) Photographs of birds with prisms.

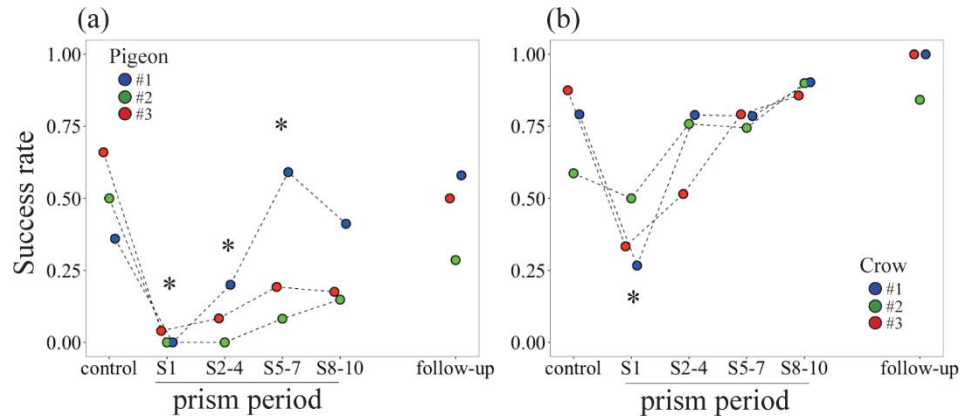


Figure 2. Success rates of food ingestion across phases in pigeons (a) and crows (b). Plots with different colours represent different individuals. Asterisks indicate a significant decrease in pecking success compared to the control phase at the group level, using the 95% confidence intervals following GLMM analyses.

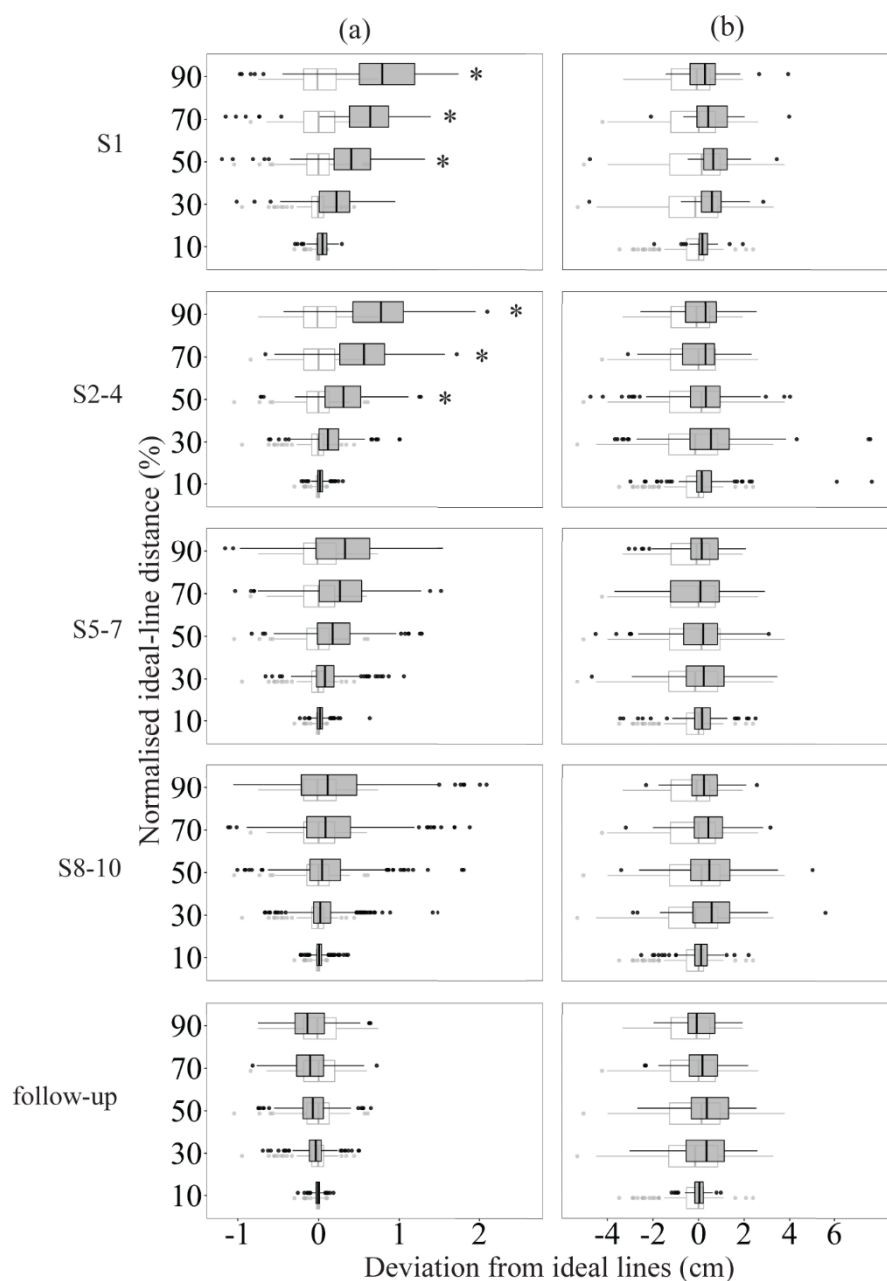


Figure 3. Lateral deviation from the ideal line across the entire course of the movement in pigeons (a) and crows (b). Deviations are represented at the normalised distance points from initiation (0%) to completion (100%). Positive and negative values represent rightward and leftward deviations, respectively. The translucent white boxes denote the control phase. Note that the scale of deviation (horizontal axis) was different between pigeons and crows. Asterisks indicate significant differences of deviation compared to the control phase.

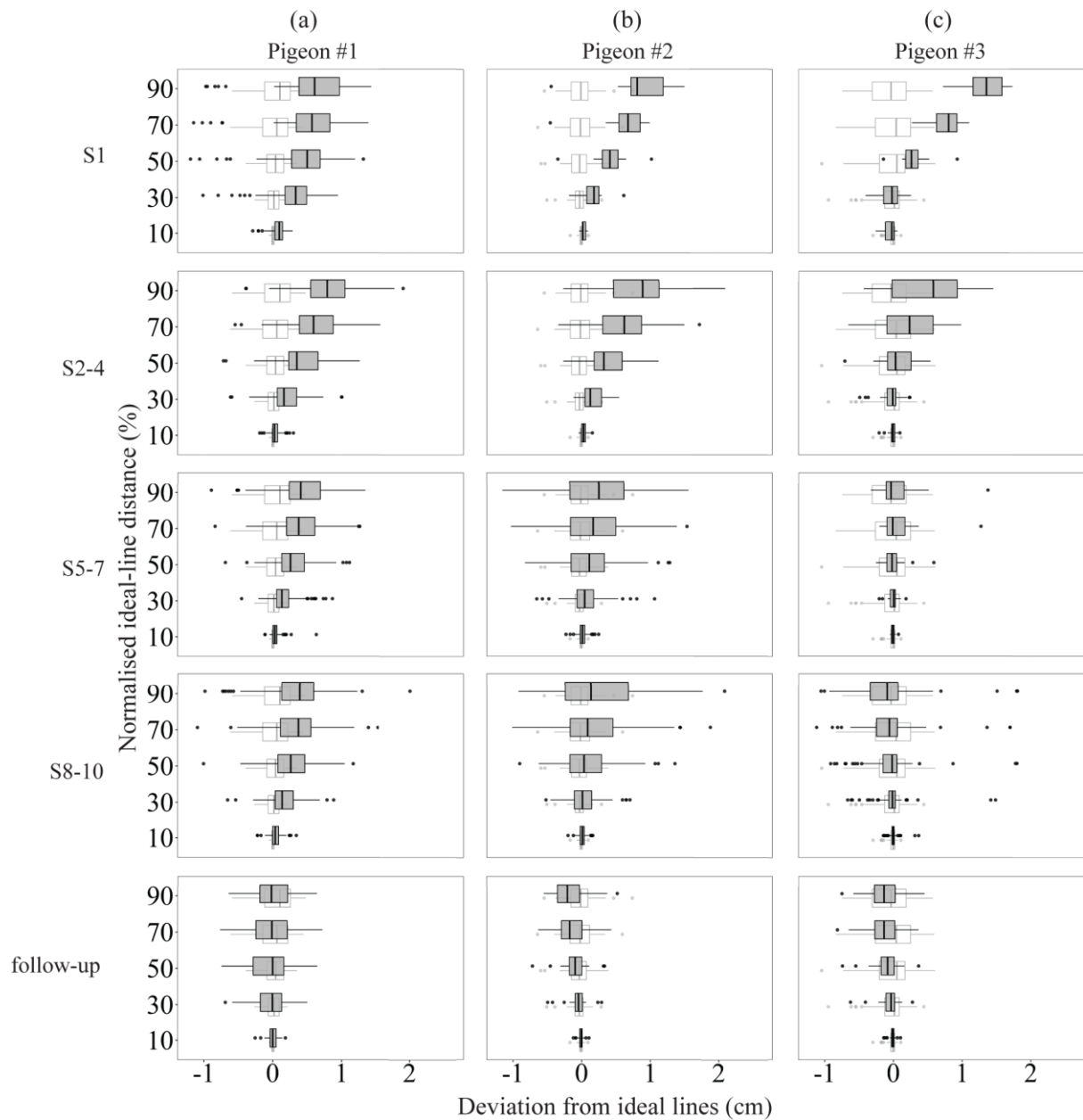


Figure 4. Individual data of lateral deviation from the ideal line across the entire course of the movement in pigeons. All three pigeons showed a rightward deviation after prism attachment, particularly in S1 and S2 – 4. Deviations are represented at the normalised distance points from initiation (0%) to completion (100%). Positive and negative values represent rightward and leftward deviations, respectively. The translucent white boxes denote the deviation of each individual in the control phase.

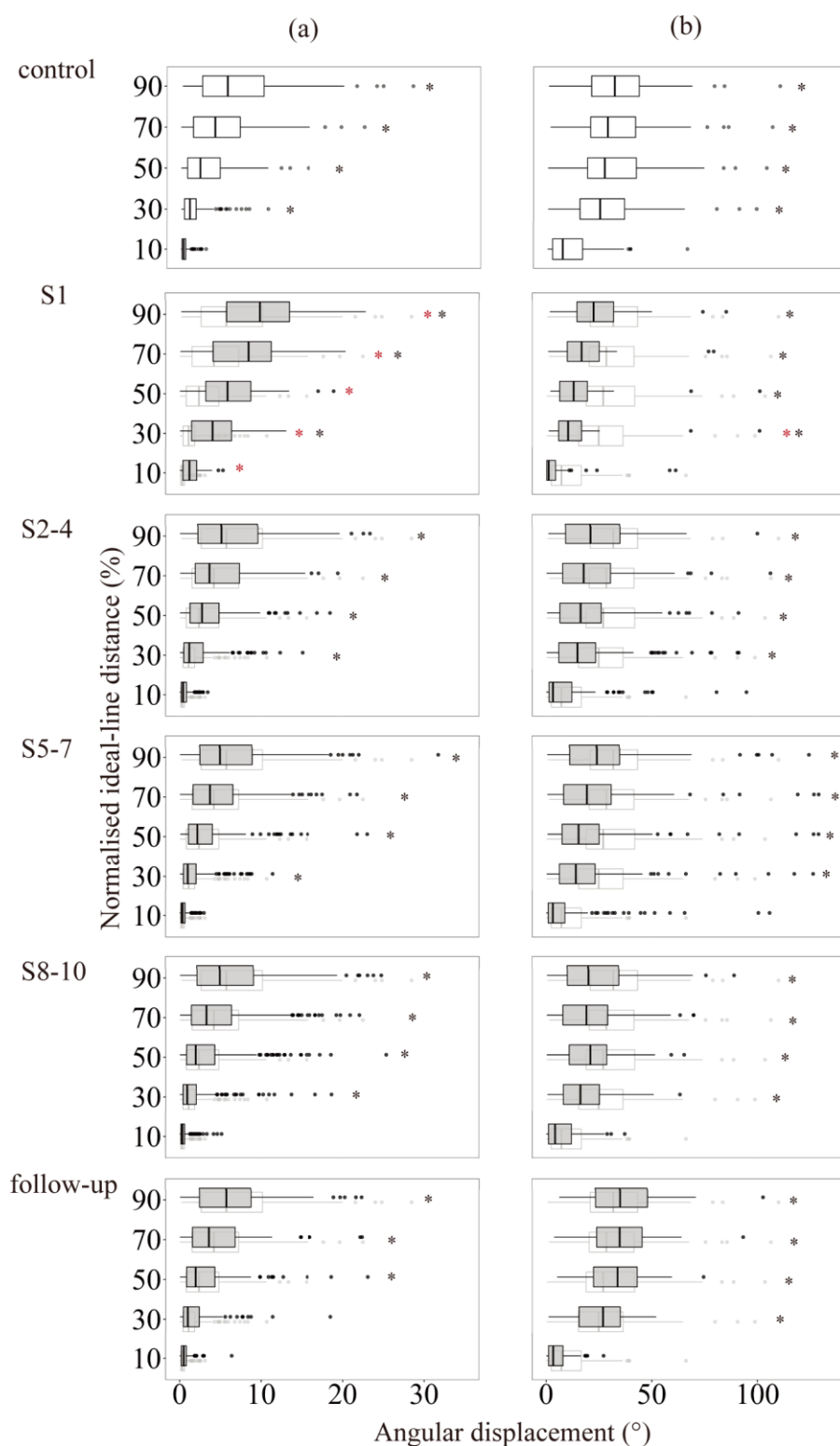


Figure 5. Angular displacement to the head/bill orientation at the initiation of pecking at the points of normalised ideal-line distance. In both pigeons (a) and crows (b), angular displacements increased from the initial point (10%) to the subsequent points (30 – 90%; black asterisks) in all the phases. Displacements after prism attachment in S1 became much larger than those in the control in pigeons (see the text for the significant main effect of the

phase). In contrast, crows showed a decrease of angular displacement, partly at the 30% point, compared to the corresponding point in the control, after prism attachment in S1 (red asterisk). Note that the scale of angular displacement (horizontal axis) was different between pigeons and crows. Black asterisks represent the significant differences between the 10% point and each of the other points (30 – 90%). Red asterisks depict the difference between the control and each of the other phases.

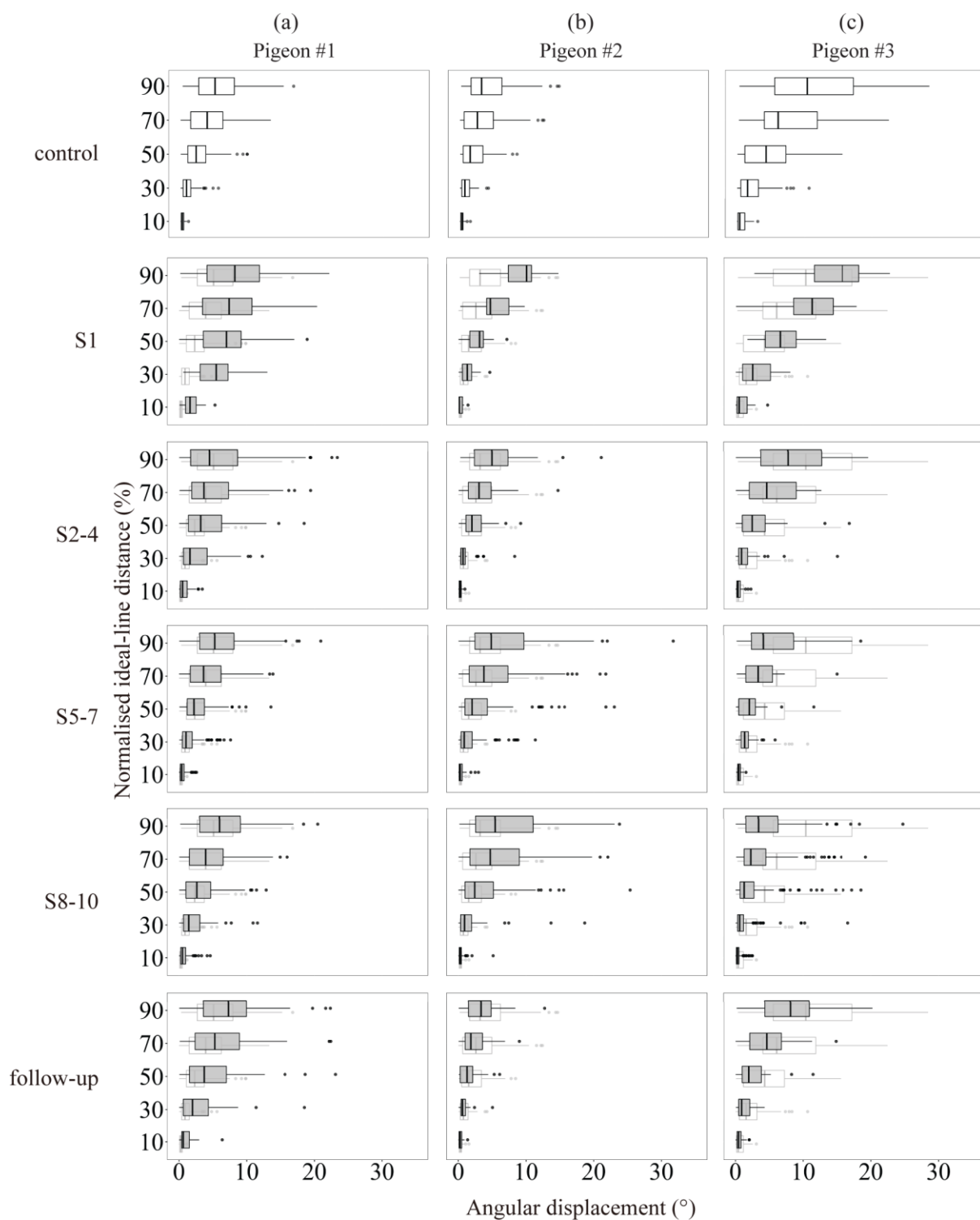


Figure 6. Individual data on angular displacement through the entire course of the movement in pigeons. All three pigeons commonly exhibited an increase of angular displacement after prism attachment, particularly in S1. Displacements are represented at the normalised distance points from initiation (0%) to completion (100%). The translucent white boxes denote the deviation of each individual in the control phase.

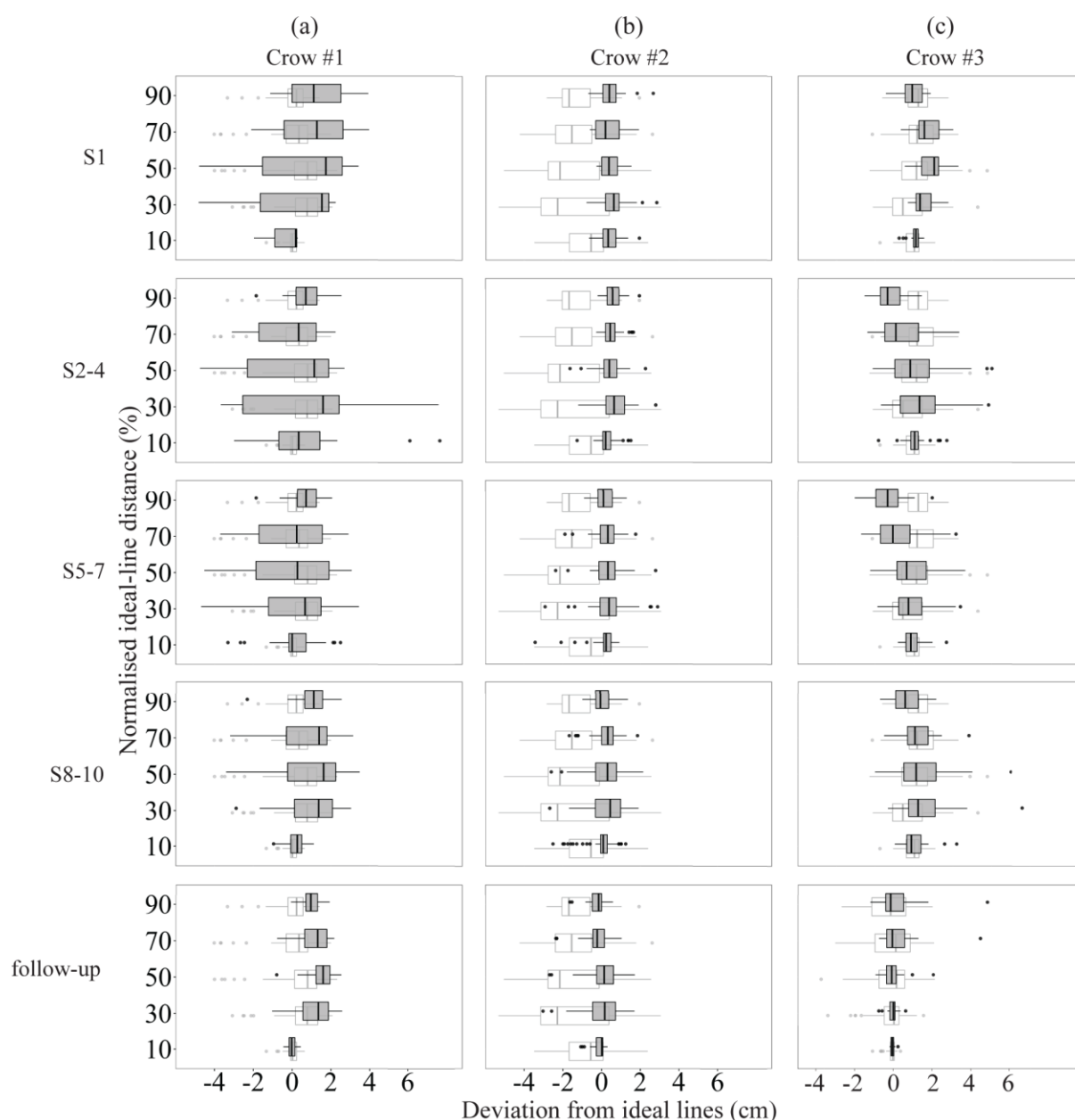


Figure 7. Individual data on lateral deviation from the ideal line through the entire course of the movement in crows. Corrections to movement deviations after prism attachment were commonly achieved but differed among individuals. Deviations are represented at the normalised distance points from initiation (0%) to completion (100%). Positive and negative values represent rightward and leftward deviations, respectively. The translucent white boxes denote the deviation of each individual in the control phase.

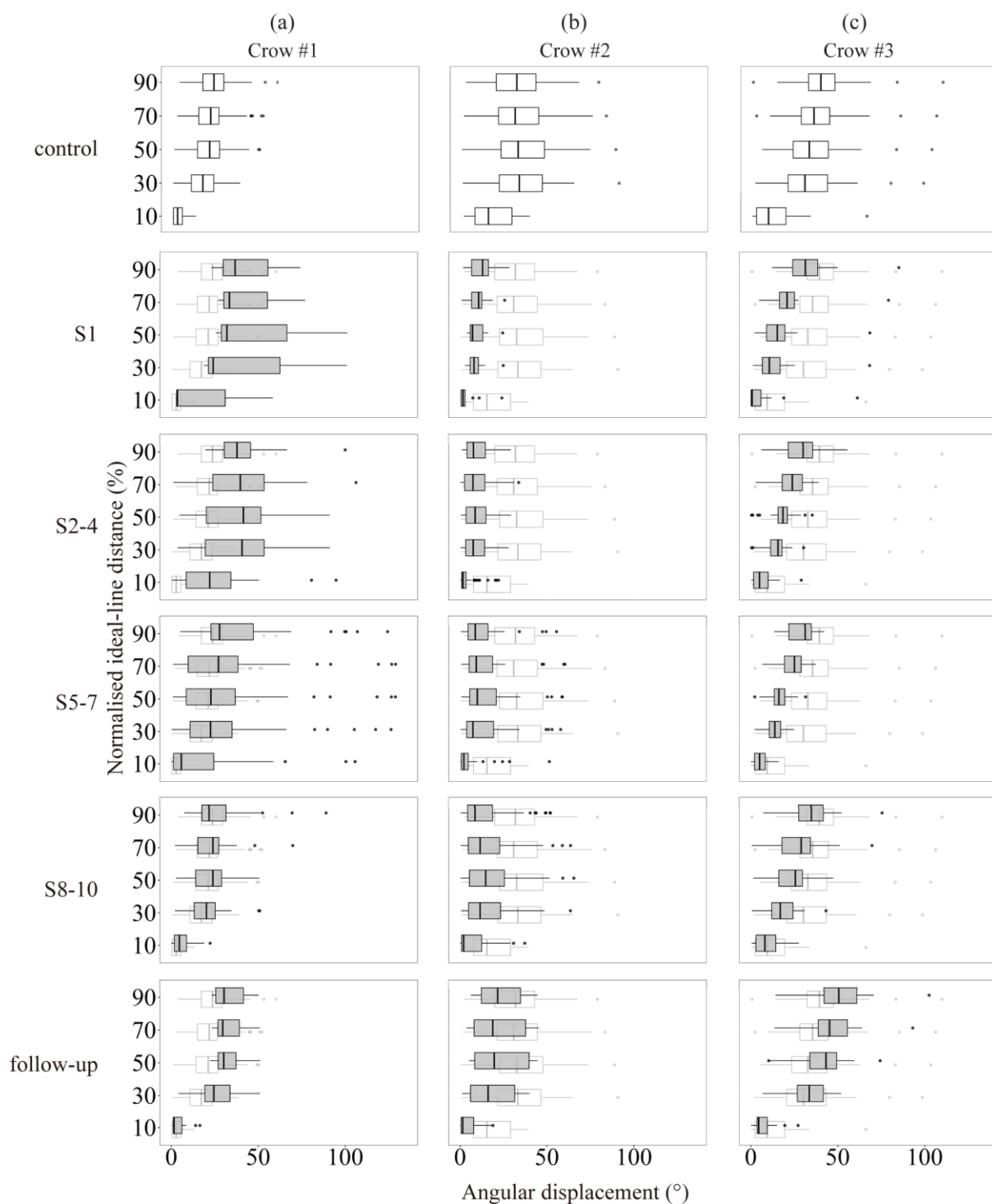


Figure 8. Individual data on angular displacement through the entire course of the movement in crows. Angular displacement was increased in crow #1 but decreased in crows #2 and #3 after prism attachment. Displacements are represented at the normalised distance points from initiation (0%) to completion (100%). The translucent white boxes denote the deviation of each individual in the control phase.

Table 1. General movement parameters

pigeon	control	S1	S2-4	S5-7	S8-10	follow-up
Movement distance (cm)	6.49±0.88	7.62±1.94	7.31±1.48	6.90±1.48	7.71±1.73	6.82±1.11
Movement duration (s)	0.073±0.015	0.101±0.038	0.088±0.034	0.087±0.048	0.100±0.048	0.070±0.020
Mean velocity (cm/s)	36.77±9.05	40.90±9.73	37.30±8.77	39.93±7.75	41.65±8.81	45.24±10.03
Peak velocity (cm/s)	51.64±12.66	57.85±15.02	53.91±12.32	61.22±13.84	57.03±12.50	65.36±14.32
Peak velocity timing (%)	59.80±13.19	57.11±17.74	62.85±16.75	65.32±18.73	63.38±19.13	72.62±14.09
crow	control	S1	S2-4	S5-7	S8-10	follow-up
Movement distance (cm)	18.11±4.55	16.21±4.52	14.18±4.61	15.64±4.80	15.53±5.10	17.02±4.94
Movement duration (s)	0.357±0.176	0.543±0.244	0.556±0.251	0.479±0.204	0.437±0.241	0.259±0.091
Mean velocity (cm/s)	45.28±16.07	23.55±11.65 *	19.88±7.51 *	26.81±10.86 *	31.75±12.90	51.22±10.52

Peak velocity (cm/s)	79.96±19.87	48.04±19.75 *	43.55±16.04 *	55.62±19.70 *	57.45±17.82	87.90±21.78
Peak velocity timing (%)	31.33±19.99	31.66±23.50	26.46±23.20	27.99±21.67	31.17±22.73	29.37±17.67

Asterisks represent the significance compared to the control using 95% CI following to linear mixed models.

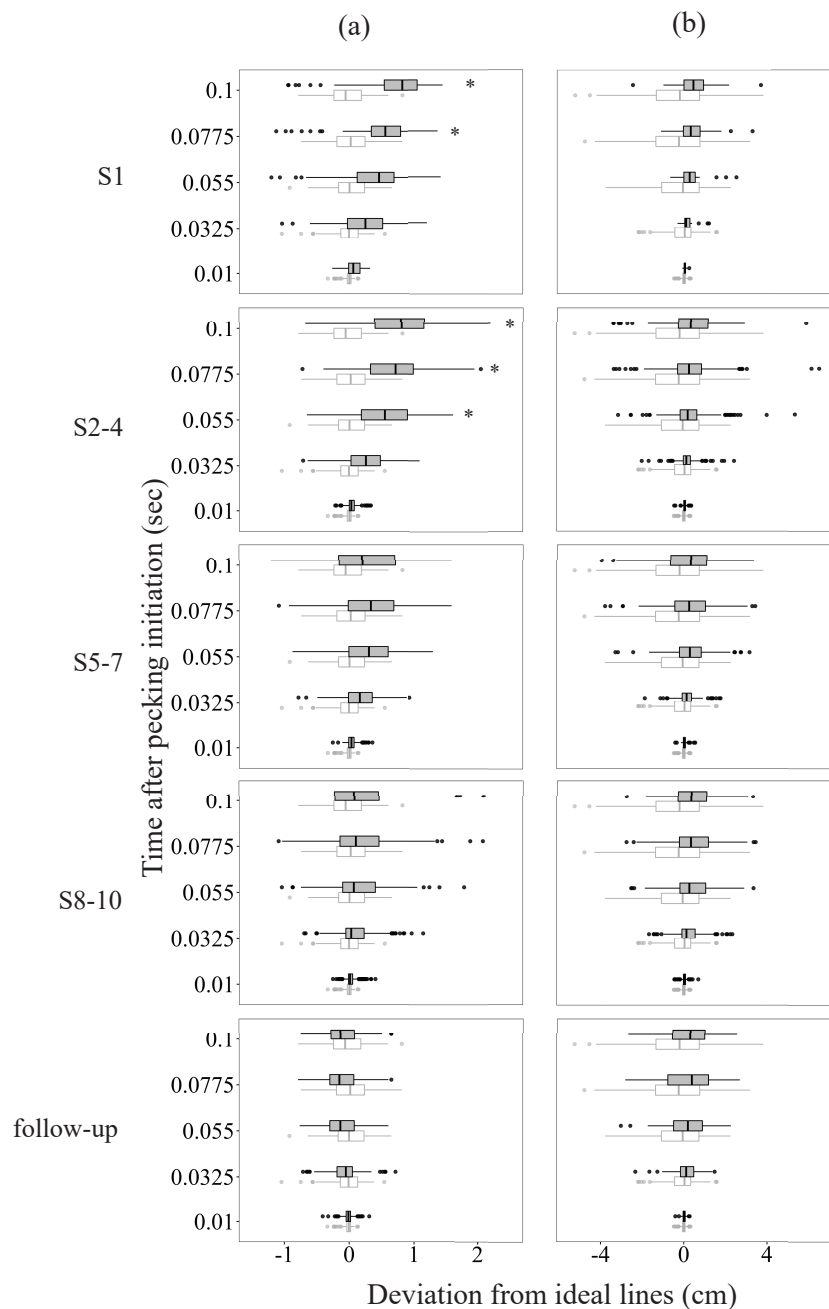


Figure S1. Lateral deviation from the ideal line during 0.1 sec after the initiation of pecking in pigeons (a) and crows (b). Positive and negative values represent rightward and leftward deviations, respectively. The translucent white boxes denote the control phase. (a) In pigeons, comparisons with 95% confidence intervals, following the confirmation of a significant interaction by a mixed model ($\chi^2 = 423.04$, $df = 20$, $p < 0.001$), revealed significant deviations (*) at the 0.1 and 0.0775 sec points in S1, and at the 0.1, 0.0775, and 0.055 sec points in the S2 – 4 phases. (b) In crows, comparisons with 95% confidence intervals, following the confirmation of a significant interaction by a mixed model ($\chi^2 = 55.28$, $df = 20$, $p < 0.002$), produced no significant deviations at any time points of any phases. Note that the scale of deviation (horizontal axis) was different between pigeons and crows.

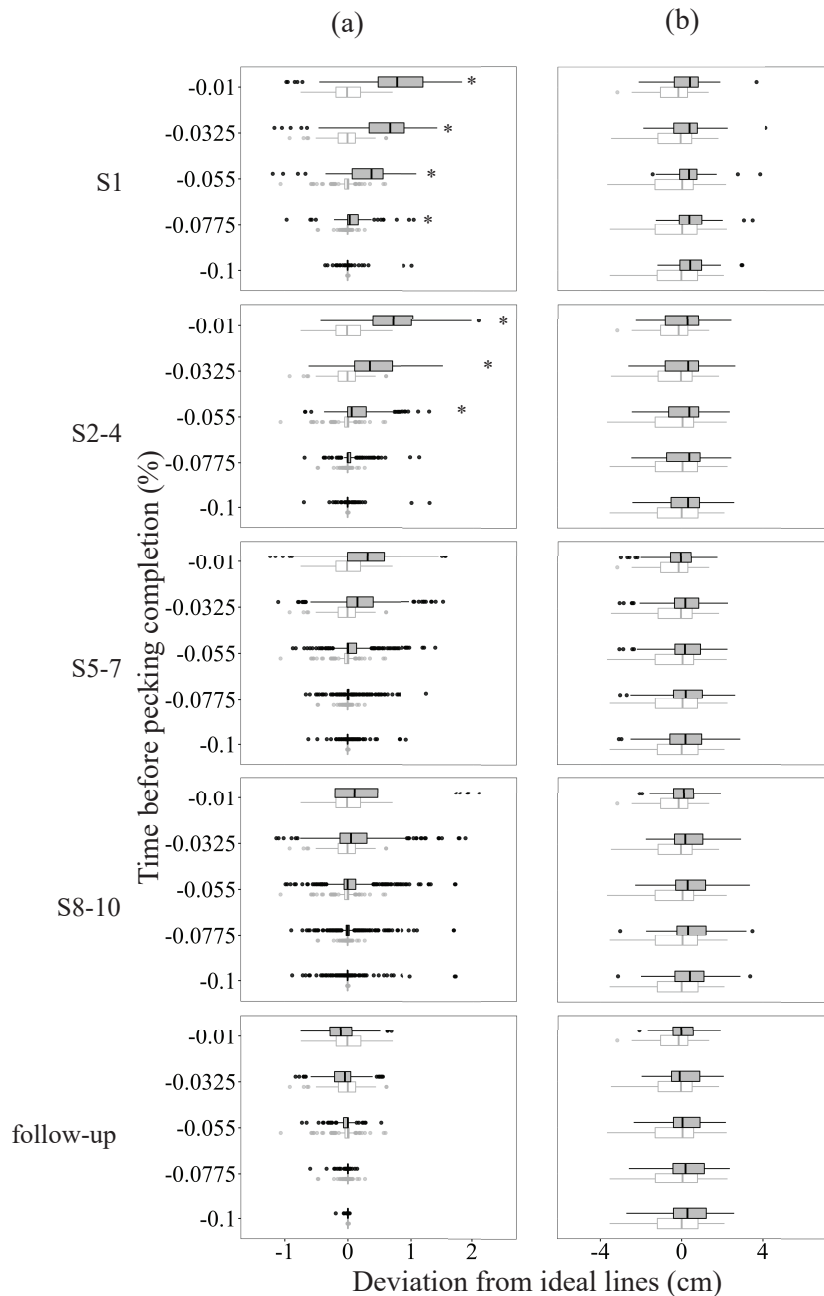


Figure S2. Lateral deviation from the ideal line during 0.1 sec before the completion of pecking in pigeons (a) and crows (b). Positive and negative values represent rightward and leftward deviations, respectively. The translucent white boxes denote control phase. (a) In pigeons, comparisons with 95% confidence intervals, following the confirmation of a significant interaction by a mixed model ($\chi^2 = 527.10$, $df = 20$, $p < 0.001$), revealed significant deviations (*) at the -0.01, -0.0325, -0.055, and -0.0775 sec points in S1, and at the -0.01, -0.0325, -0.055 sec points in the S2 – 4 phases. (b) In crows, no significant interaction was found by a mixed model analysis ($\chi^2 = 7.26$, $df = 20$, ns) and, thus, comparison with 95% confidence intervals was not applied. Note that the scale of deviation (horizontal axis) was different between pigeons and crows.

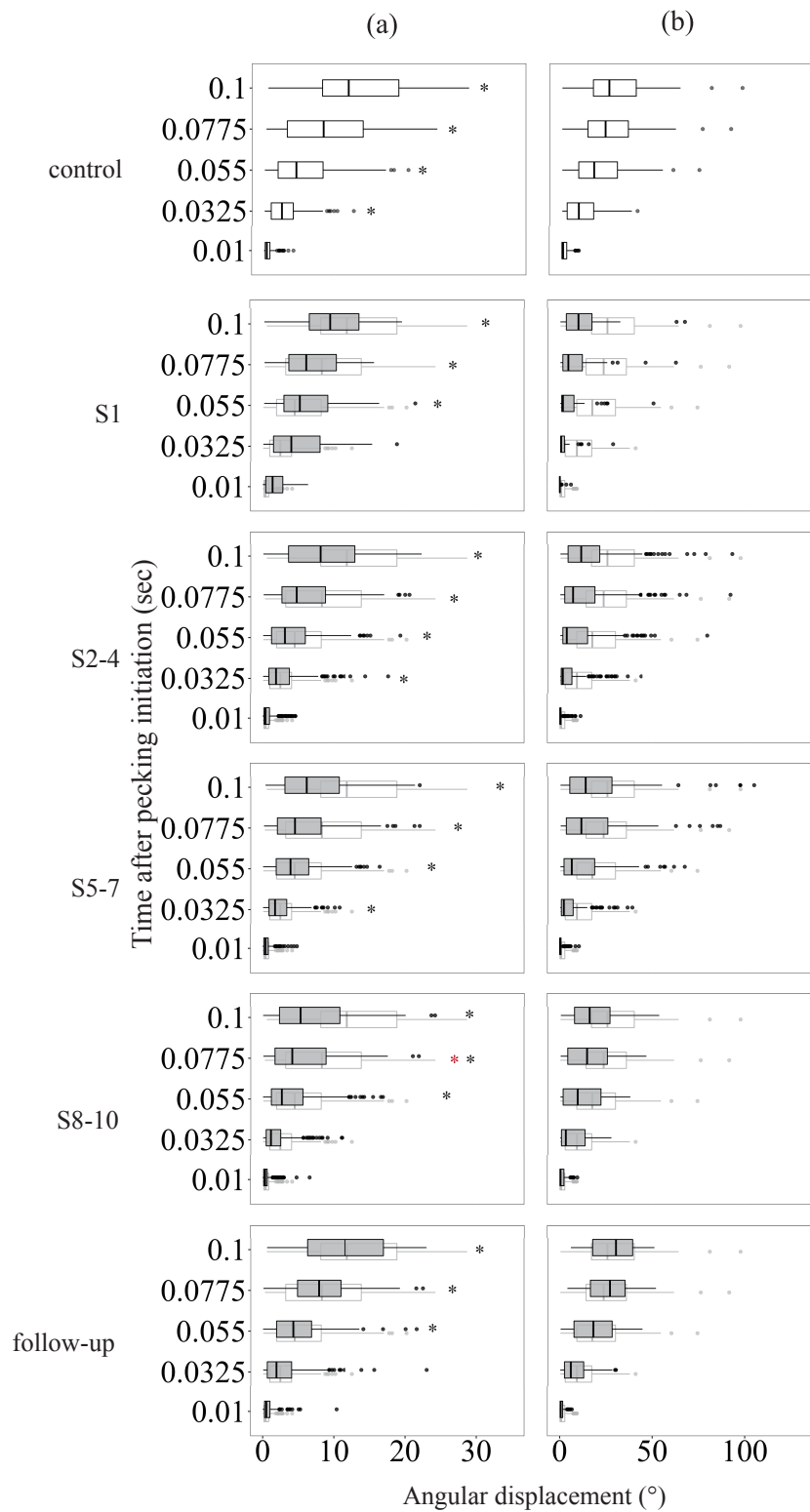


Figure S3. Angular displacement to the head/bill orientation at the initiation of pecking during 0.1 sec after initiating pecking in pigeons (a) and crows (b). The translucent white boxes denote the control phase. (a) In pigeons, a mixed model analysis produced a significant interaction ($\chi^2 = 43.22$, $df = 20$, $p < 0.002$). Comparisons with 95% confidence intervals revealed that angular displacements to the initial head/bill orientation were larger at the time points 0.055, 0.0775, and 0.1 sec, than at 0.01 sec, consistently in all the phases (black asterisks). At only one time point (0.0775 sec), the angular displacement in S8 – 10 was smaller than that in the control (red asterisk). (b) In crows, a mixed model analysis produced significant main effects for the phase ($\chi^2 = 280.21$, $df = 5$, $p < 0.001$) and the time variables ($\chi^2 = 2335.69$, $df = 4$, $p < 0.001$) with no significant interactions ($\chi^2 = 19.15$, $df = 20$, $p = 0.512$, *ns*). For the main effect of the phase variable, the significant decrease of angular displacement was found only in S1 in comparison to the control. Note that the scale of angular displacement (horizontal axis) was different between pigeons and crows.

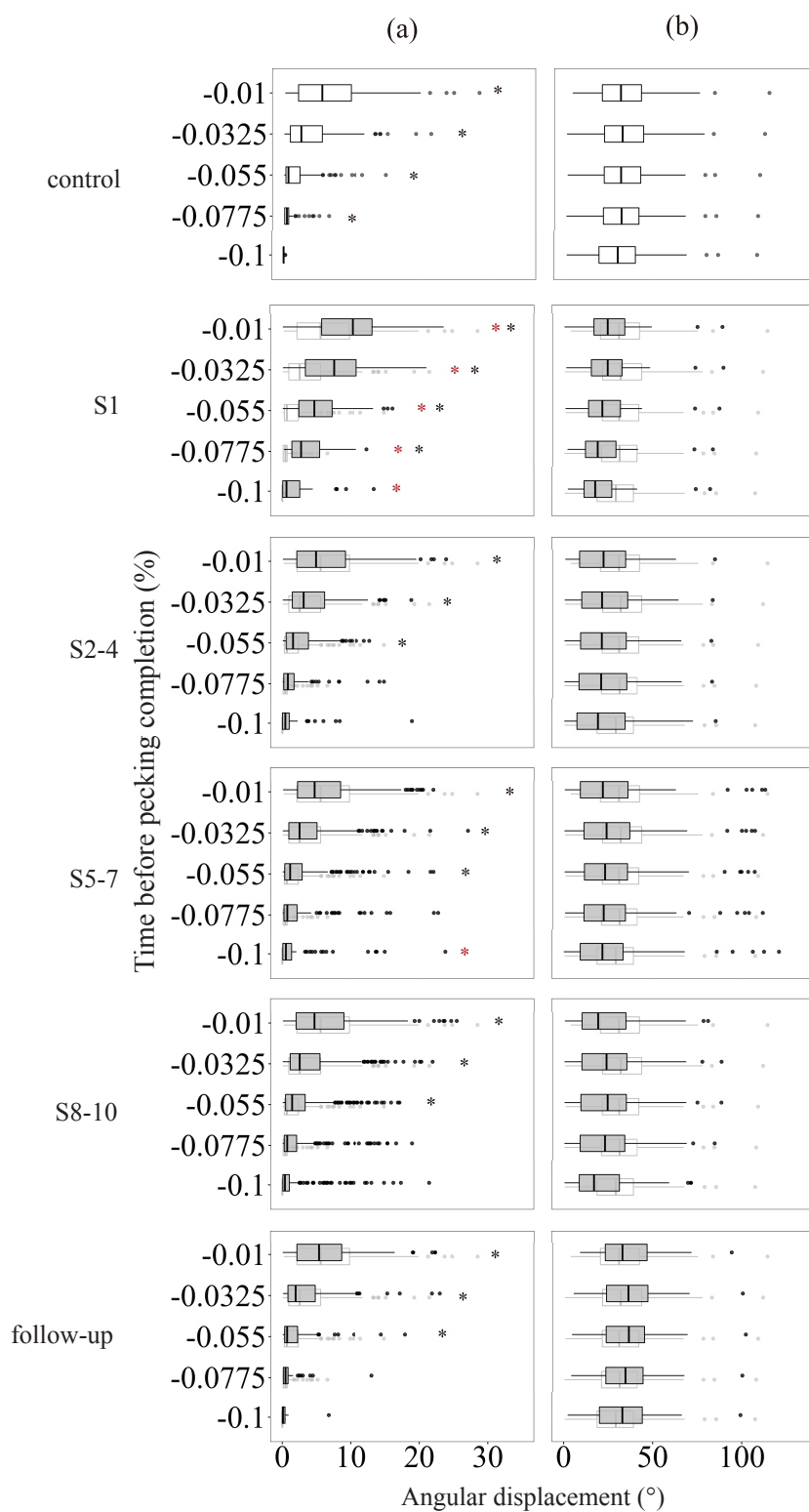


Figure S4. Angular displacement to the head/bill orientation during 0.1 sec before the completion of pecking in pigeons (a) and crows (b). The translucent white boxes denote the control phase. (a) In pigeons, a mixed model analysis produced a significant interaction ($\chi^2 = 83.85$, $df = 20$, $p < 0.001$). Comparisons with 95% confidence intervals revealed that angular displacements to the initial head/bill orientation were larger at the time points -0.01, -0.0325, -0.055 sec, than at -0.1 sec, consistently in all the phases (with black asterisk). A significant difference among phases was found only at the -0.1 sec point in S5 – 7, where the displacement was larger than in the control (with red asterisk). (b) In crows, a mixed model analysis yielded the significant main effect of only the phase variable ($\chi^2 = 174.00$, $df = 5$, $p < 0.001$) with no significant interaction between the phase and the time ($\chi^2 = 4.11$, $df = 20$, $p = 0.999$, *ns*). For the main effect of the phase variable, however, no significant difference was found between the control and any phases using 95% confidence intervals. Note that the scale of angular displacement (horizontal axis) was different between pigeons and crows.

Table S1. Individual data of corrective pecking trials

individual	crow			pigeon		
	#1	#2	#3	#1	#2	#3
S1	1/2	0/1	1/1	0	0	0
S2-4	7/10	0	0	0/2	0/5	0
S5-7	0	0	1/1	0/32	0/14	0
S8-10	2/2	0	0	0/4	0/9	0

Values on the left and right on each cell denote success and total numbers of corrective pecking trials, respectively.