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SHORT COMMUNICATION

Pigeons (*Columba livia*) fail to connect dots in learning biological motion

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Abstract Biological motion point-light displays provide a powerful method for studying motion perception. Non-human animals are capable of discriminating point-light displays, but it remains unknown how they perceive biological motion in these displays. We trained two groups of pigeons to discriminate video stimuli using two different classification rules. The motion-congruent group was trained to discriminate full-detail and corresponding point-light displays of pigeons from full-detail and point-light displays of humans. The motion-incongruent group was trained to discriminate full-detail pigeons and point-light humans from the other displays. Both groups acquired the discrimination. When tested with novel displays, pigeons showed good transfer of learning. Transfer was poorest with the point-light displays in the motion-congruent group. The results indicate that the pigeons failed to make the connection between the full-detail displays and their point-light counterparts even when the common motion was available as a cue.

Keywords Motion discrimination · Point-light displays · Biological motion · Pigeons

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Introduction

Motion is a biologically important source of information for animals. Comparative examinations using video technology have revealed that motion has properties that emerge from a rapid series of static frames (Cook and Roberts 2007) which may not be present among static frames (Dittrich and Lea 1993; Cook and Katz 1999). Pigeons are capable of discriminating conspecific individuals based on their actions and can generalize this differentiation to novel stimuli (Jitsumori et al. 1999; Yamamoto and Watanabe 2007), whereas comparable discrimination is difficult without motion (Watanabe and Ito 1991; Ryan and Lea 1994).

Point-light displays are an effective means of investigating the use of motion in isolation from other visual cues. Seemingly, vivid percepts of human body movements are reported by human viewers when presented with moving point lights attached to principal positions of the human body. This happens even with removal of the pictorial cues outlining the shape of a body; a changing point-light configuration projects as an animate object that visibly moves against a blank background (Johansson 1973). Also, non-human animals can discriminate among different motions in such point-light displays (e.g. Blake 1993; Dittrich et al. 1998; Regolin et al. 2000; Tomonaga 2001; Parron et al. 2007; Brown et al. 2010; MacKinnon et al. 2010; Troje and Aust 2013; Nakayasu and Watanabe 2014). However, non-human animals differ from humans in terms of how they perceptually group multiple elements into a configuration (Qadri and Cook 2015), and it remains unknown whether animals discriminate impoverished point-light displays using the same motion cues as they use in responding to similar full-detail motion displays.

Using a go/no-go discrimination procedure, Dittrich et al. (1998) trained pigeons to discriminate different patterns of

conspecific movements. The training movements involved motions such as pecking and walking, all presented as full-detail displays; it was followed by transfer (test) movements that were presented as point-light displays. In other conditions, birds were trained on point-light displays; then, they were tested with full-detail displays. Dittrich et al. discovered that three of eight pigeons trained with the full-detail displays pecked positive test stimuli (S+) more than negative stimuli (S−), indicating successful discrimination. Although they generally pecked point-light versions of S+ more than those of S−, this peck rate disparity was small. In contrast, four of eight pigeons trained with the point-light displays pecked more S+ than S− in training, but none of these birds showed differential peck rates to the full-detail test displays. One interpretation for such unidirectional transfer is that pictorial cues in the full-detail displays facilitate perceptual grouping of multiple point lights into a single unity, which may be otherwise difficult to perceive. A more recent study also demonstrated that pigeons trained to discriminate two different actions of dogs and bucks in full-detail displays failed to transfer this learning to point-light ones (Qadri et al. 2014).

In the present study, we examined whether pigeons learn to discriminate motion categories using the same motion cues in point-light and full-detail displays when simultaneously trained with these two display types. Previous studies have reported that pigeons acquired a discrimination faster and transferred better when categorizing stimuli that fit into natural categories, such as food versus nonfood, than when categorizing the same stimuli that belonged to arbitrary groupings (Wasserman et al. 1988; Watanabe 1993). We adapted such a natural versus pseudocategory discrimination paradigm and divided pigeons into two groups. The motion-congruent group was trained to discriminate full-detail and corresponding point-light displays of pigeons from corresponding displays of humans. The motion-incongruent group was trained to discriminate full-detail displays of pigeons and point-light displays of humans from point-light displays of pigeons and full-detail displays of humans. After attaining the discrimination, both groups were tested with the same novel test stimuli. Thus, if pigeons perceive biological motion in the point-light displays as they do when observing full-detail displays, and if they use this discriminative cue, then the motion-congruent group should acquire the discrimination faster and show better transfer than the motion-incongruent group.

Methods

Subjects

Six pigeons (*Columba livia*) were used as subjects. They were kept individually in cages under a 12:12 h light/dark cycle. Water was freely available in the cages. They were

maintained at 80 % of their free feeding weight throughout the experimental period. The Animal Care and Use Committee of Keio University (No. 08008) approved the experiment reported here.

Apparatus

The experiment was conducted in an operant chamber. A computer monitor (EP51G, BenQ) equipped with an infrared touch screen frame (Unitouch, Touch Panel Systems) was placed on the front panel. Three 45-mg precision pellets were delivered into a feeder tray positioned below the monitor. A PC-compatible computer (Dimension 1100/B100, Dell) controlled the experimental events and operated the house light, feeder light, and dispenser, running an experimental program written in Microsoft Visual Basic 6.

Stimuli

The stimuli were 16 video clips (9.6 × 6.4 cm, 29 fps) presented centrally on the monitor against a plain background. These videos are available in supplementary materials. Each of the eight clips depicted a monochromatic video of a human dancer or a pigeon in both presented as full-detail (FD) type of display; eight other videos were a point-light (PL) type of display corresponding to (i.e., created from) respective full-detail displays, consisting of 17 moving dots on the dancer and the pigeon. Half of the videos in each type showed a professional dancer performing actions such as stepping, jumping, and swinging, and the remaining videos showed pigeon movements, including walking, pecking, and wing flapping. The choice of these motion categories was arbitrary, but all movements were editable into 2-s video clips. Two of four clips of each display type (FD, PL) were used as training stimuli, and the remaining were used as test stimuli. Each movie was 2 s in duration and was repeated for 20 s on each trial.

Procedure

Discrimination training

Pigeons were first trained to peck the stimuli on the monitor. They were divided into two groups of three birds each. Birds in motion-congruent group were trained to discriminate the full-detail and point-light displays of pigeons from corresponding displays of human motions: Pecks to the pigeon videos were reinforced (S+), whereas pecks to human stimuli were not (S−). Birds in motion-incongruent group were trained to discriminate full-detail pigeons and point-light humans (S+) from point-light pigeons and full-

detail humans (S−). Each trial began with a peck to the start stimulus (a white circle). This was replaced by one of the videos. Pecks during an S+ trial were reinforced on a variable interval 8-s schedule, whereas responses during an S− trial were not reinforced. Trials were separated by an inter-trial interval of 5 s.

Each daily session consisted of 80 trials or a session was terminated after 120 min, whichever came first. Eight training stimuli were presented ten times each. In each session, each S+ stimulus was presented in a nonreinforced trial, termed a probe trial, in order to measure S+ peck rates without the intervention of food delivery. The stimulus presentation followed a pseudorandom order with the constraint that neither S+ nor S− stimuli appeared in more than three successive trials. The discrimination training continued for at least 20 sessions, until the subjects achieved a discrimination ratio for both display types (mean pecks to the S+ stimuli during probe trials divided by mean pecks during S− trials) of above 0.90 in three consecutive sessions. In order to avoid overtraining on either stimulus type, no more than 30 training sessions were provided.

Test

Upon attainment of the training criterion, pigeons received 10 test sessions. Each test session consisted of 96 trials which included repeated presentations of stimuli from the training session interleaved with novel test stimuli. The eight training stimuli were each presented 11 times. In addition, eight novel video clips of pigeon and human actions were intermixed among the training trials and presented one time each as test trials. Subjects were not given any reinforcement during test trials.

Results

Figure 1a shows the first 20 acquisition sessions (each block reflects the average ratio over four sessions). Number of sessions to reach criterion were 16, 24, and 30 for birds in the congruent group and 14, 22, and 23 for birds in the incongruent group. No group difference was found ($t(4) = 0.74$, $p = .50$). In both groups, the discrimination ratio was consistently higher with the full-detail displays than with the point-light displays. This result was confirmed using a linear mixed-model, with subject as a random factor, which revealed significant main effects of display type, a between-subject variable, $F_{1,36} = 28.67$, $p < .001$, and session block, a repeated measures variable, $F_{4,36} = 13.76$, $p < .001$. No other main effects or interactions were significant.
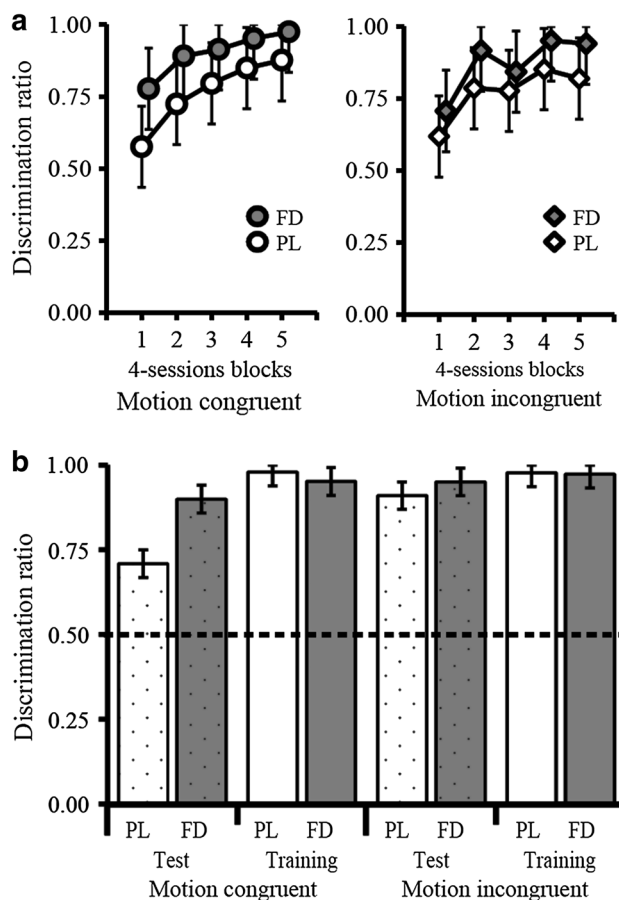
Fig. 1 Discrimination ratios for **a** acquisition and **b** generalization tests. *PL* and *FD* indicate point-light and full-detail displays, respectively. *Error bars* indicate 95 % confidence intervals

We then evaluated the birds' performance on the generalization test (Fig. 1b). To analyze the test session data, a discrimination ratio was calculated by dividing the number of novel S+ pecks for each particular display type by each bird's total number of pecks toward both S+ and S− stimuli of the display type (Table 1 shows mean response rates across all test sessions). Overall, birds in both groups showed transfer to novel stimuli, with the discrimination ratio above chance (.50), confirmed using one-sample *t* tests in the congruent group (point-light display: $t(2) = 9.77$, $p = .01$ and full-detail display: $t(2) = 158.43$, $p < .001$) and the incongruent group (point-light display: $t(2) = 13.77$, $p = .005$ and full-detail display: $t(2) = 104.18$, $p < .001$), although discrimination was poorer with the novel stimuli than with training ones. The motion-congruent group showed poorer transfer than the incongruent group, but both groups showed consistently worse transfer to the point-light displays than to full-detail ones. A linear mixed-model with subject as a random factor confirmed these results by showing significant main effects of group ($F_{1,4} = 10.50$, $p = .032$), experience

Table 1 Mean response rates toward both S+ and S− stimuli during 20-s trials in 20 test sessions

Group	Subject	Training				Test			
		PL		FD		PL		FD	
		S+	S−	S+	S−	S+	S−	S+	S−
Motion congruent	A22	22.00	0.85	14.40	0.10	20.35	8.70	13.00	0.20
	Charles	18.75	1.40	23.35	0.90	23.25	7.80	22.80	0.55
	Franz	19.25	3.80	23.35	0.60	17.75	8.50	25.60	0.65
Motion incongruent	C13	35.10	1.30	27.45	0.45	16.70	1.75	24.20	1.20
	C23	23.20	1.25	34.75	0.95	12.05	2.20	37.80	1.65
	Nerva	25.80	1.75	17.55	0.70	19.00	1.10	16.65	1.00

PL and FD indicate point-light and full-detail displays, respectively

(training or test; $F_{1,12} = 27.32$, $p < .001$) and stimulus type ($F_{1,12} = 63.26$, $p < .001$). All two-way interactions were significant ($Fs > 5.90$, $p < .05$), and three-way interaction was also significant ($F_{1,12} = 11.10$, $p = .006$). Post hoc analyses indicated that discrimination ratios to novel stimuli in the point-light display were significantly higher in the incongruent group than in the congruent group ($p < .001$), whereas the difference in the full-detail display was not significant ($p = .317$). No group difference was found in mean peck rates to the training stimuli.

Discussion

Our results demonstrate that pigeons are capable of learning to discriminate point-light displays, although learning rates for these displays were lower than those observed for the full-detail displays from which the point-light displays were derived. Previous studies reported that pigeons failed to transfer motion discrimination to point-light displays (Dittrich et al. 1998; Qadri et al. 2014). In those studies, the overall dissimilarity of point-light and full-detail displays greatly reduced peck rates to the point-light displays during transfer tests, resulting in poor discrimination of the point-light test stimuli. In contrast, in the present study, where pigeons were trained with both point-light and full-detail displays, their peck rates to the test stimuli were well maintained.

Pigeons also showed transfer of this discrimination to novel stimuli, including point-light displays. However, contrary to our hypothesis, the shared motion between two types of displays (PL and FD) did not facilitate discrimination learning, suggesting that learning of the biological motion of a full-detail display is independent from the learning of that of a point-light display. The motion-congruent group showed worse discrimination ratios with the point-light displays compared with the motion-incongruent group. An examination of peck rates showed that the less successful transfer in the motion-congruent group was

likely due to relatively high peck rates to the novel point-light S− stimuli (Table 1). In contrast, peck rates to the novel point-light S+ decreased for the three pigeons in the motion-incongruent group.

In order to examine such group difference in detail, we analyzed all point-light video clips by calculating total motion paths of all dots, mean speed of 17 dots, and x- and y-ranges of dot movements, as well as visualizing motion paths (Table S1). One of the test point-light humans (Stimulus g in Table S1) had similar motion paths to the training point-light pigeons, and birds in both groups appeared to respond to it as a point-light pigeon (Table S2). However, no single parameter seems to explain the relatively high peck rates of the motion-congruent group to the other point-light human (Stimulus h in Table S1).

In summary, consistent with previous studies (Dittrich et al. 1998; Qadri et al. 2014), the present study provides another case in which the pigeons, unlike humans, seem to fail to make the connection between the full-detail displays and their point-light counterparts even if the common motion features of stimuli are available as a cue. Contrary to our prediction, the motion-congruent group showed poorer transfer to point-light displays compared with the motion-incongruent group. We speculated that this group difference could be explained by the fact that the motion paths of one of the test stimuli reflecting human motion were similar to those of the pigeon motions used in training, although the exact cause remains unsolved. What pigeons attend to in the point-light displays warrants further investigation.

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