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DISCRIMINATION OF DIRECTION OF MOVEMENTS IN PIGEONS FOLLOWING PREVIOUS EXPERIENCE OF MOTION/STATIC DISCRIMINATION

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Two experiments examined pigeons' discrimination of directional movement using pictorial images shown on computer monitors. Stimuli consisted of the movement of a bird against a stationary background or the movement of the background behind a stationary bird. In Experiment 1, pigeons were trained to discriminate either leftward or rightward motion of either the bird or the background from stationary frames drawn from the same movies. The background-discrimination group acquired the discrimination faster than the bird-discrimination group. In Experiment 2, transfer of the discrimination from the task of Experiment 1 to a discrimination between motion directions was examined. Most of the pigeons learned this discrimination rapidly, whereas in a pilot study in which direction discrimination was trained without previous static/movement discrimination, learning was poor. It appears that an experimental history of movement against stationary discrimination promoted the pigeons' learning of the directional motion discrimination.

Key words: motion, motion perception, discrimination, salience, key peck, pigeons

Motion perception is an important ability for animals. Most important objects in their natural environments, such as other animals, move, and it is necessary for animals to detect and discriminate among such movements to interact socially with conspecifics, to escape from their predators, to catch prey, and to move efficiently within their environments. Therefore, movement provides essential information for survival in nature whereas static objects or background may be less valuable or dangerous and therefore may be less likely to control responding. Dittrich and Lea (1993) examined the salience of motion compared with stationary images in pigeons. Pigeons were trained to discriminate between video clips containing various movements of pigeons and stationary frames drawn from the same videos. In their experiment, the pigeons in a movement-positive group learned the task easily whereas the pigeons in a movement-negative group showed no discrimination (though evidence of discrimination was found under extinction conditions). This finding of a feature-positive effect (Jenkins & Sainsbury, 1970) in motion implies that motion is a salient feature of the visual scene for pigeons.

Motion perception studies in pigeons have also indicated that they are capable of discriminating not only complex patterns of motion (e.g., Emmerton, 1986), but also different categories of motion in a variety of types of stimuli. For example, Dittrich, Lea, Barrett, and Gurr (1998) demonstrated that pigeons discriminated different types of movement of pigeons (walking and pecking), whether they were presented in normal fully detailed video images or as ''biological motion'' stimuli consisting of a few moving dots. Jitsumori, Natori, and Okuyama (1999; Experiment 4) reported that pigeons discriminated 2 different individual pigeons using videos.

Moreover, categorization of motion patterns is not restricted to conspecific motion. Cook, Shaw, and Blaisdell (2001) successfully trained pigeons to discriminate two different types of relative motion in computer-generated stimuli. In one type of stimulus, the camera's perspective went around an approaching virtual arch whereas it went through the approaching arch in the other stimuli. Goto, Lea, and Dittrich (2002) also reported that converging ''intentional'' motion paths were discriminated from random dot motion paths by pigeons. In their Experiment 1, Goto et al. trained pigeons to discriminate stimuli con-

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taining four randomly moving dots from similar stimuli in which one dot moved nonrandomly, "tracking" or "stalking" one of the randomly moving dots. Though the pigeons' discrimination was above chance level, they did not reach the training criterion. In Goto et al.'s Experiment 2, the task was changed to the discrimination of three dots stalking one target from four dots moving randomly. The pigeons trained with the stimuli containing the stalking dots as positive stimuli maintained their discrimination, whereas the pigeons for which the stalking dots were negative stimuli lost their discrimination, implying a kind of feature-positive effect.

These studies imply that pigeons can differentiate motion patterns that fall into categories defined by human experimenters. If the patterns of motion were similar to each other, however, the discrimination of motion might well become difficult even though it would be easy for humans to discriminate. A good example is discrimination of direction of motion. In a pilot study, we attempted to train two groups of 6 pigeons to discriminate rightward from leftward directional motion either of an image of a bird or of naturalistic scenery (the stimuli and experimental conditions in the pilot study were exactly the same as in Experiment 2 of the present study), but only 2 out of 12 pigeons acquired the discrimination within a total of 60 sessions using two different training procedures. Discrimination of direction is a particularly interesting case because the static information available to the subject is identical for the two stimuli, so any discrimination must depend on movement alone. In the present study, therefore, we sought a more powerful technique to examine discrimination of directional motion in pigeons.

To the human eye, an important aspect of the organization of a visual scene is segmentation of the scene into figure and ground. Movement of a foreground object relative to a background provides a strong cue to support such segmentation, and for many purposes the important question is how figure and ground move relative to each other, rather than the absolute direction in which either of them moves. It is not known whether the same principles of organization apply in pigeon vision, though there are indications from the difficulty of training pigeons to recognize occluded objects that segmentation of figure and ground may not be as spontaneous in avian as in human vision (cf. DiPietro, Wasserman, & Young, 2002). Furthermore, where a stimulus is segmented into a figure and ground that move relative to each other, for many purposes it is unimportant which of them moves relative to an external frame of reference, and indeed the human eye is easily confused between foreground and background movement. It is not known, however, whether the same dominance of relative over absolute motion applies to other species.

For both of these reasons, in the experiments described here, we always trained some pigeons with stimuli involving movement of a foreground object, and other pigeons with stimuli involving movement of a background, in order to see whether foreground motion would enjoy the same salience as it does for humans.

In Experiment 1, pigeons were trained to discriminate either leftward or rightward directional motion of a bird or a background from stationary frames extracted from the identical movies. The stimuli consisted of a bird superimposed in a background, and only one of these (bird or background) was moved in any one stimulus. Subsequently, transfer between moving bird and moving background stimuli was tested to examine what aspects of the motion stimuli controlled behavior. In Experiment 2, the same pigeons were trained on the discrimination of leftward and rightward motion, that only 2 out of 12 pigeons in our pilot study had learned, to examine whether the experimental history of motion-static discrimination facilitated the acquisition of directional motion discrimination.

EXPERIMENT 1

The first aim of this experiment was to replicate the result of Dittrich and Lea (1993) that had indicated that pigeons discriminated movies from the static frames of which they are constructed. This was necessary to confirm that the particular motion stimuli we were using were readily discriminated. Pigeons were trained to discriminate a directional motion from stationary frames extracted from the moving stimulus. When the discrimination was established, generalization tests were given to the pigeons to examine transfer to different patterns of motion. The transfer tests allowed an initial test of discrimination between motion directions because in the absence of such discrimination there should be no difference between transfer to new stimuli involving movement in the same direction as in training, and to new stimuli involving movement in the opposite direction.

The specific questions addressed in this experiment were (a) whether pigeons could discriminate motion in the stimuli designed for this experiment, (b) whether there is a difference of the acquisition speed between bird-motion and background-motion discrimination groups, (c) whether the directional motion used for positive stimuli in the training session evokes more responses in a generalization test than the directional motion that had not been used in the training sessions, and (d) whether relative motion in the trained direction evokes more responses in a generalization test than absolute motion in that direction.

METHOD

Subjects

Twelve pigeons (*Columba livia*) obtained as discards from local fanciers were used as subjects in this experiment. They were normally housed in two indoor aviaries measuring 2.2 m by 3.4 m by 2.4 m. Each aviary was equipped with pigeonholes in units of 16, and free access to water and crushed oyster shells was available. The pigeons were maintained on a 12:12 hr light/dark cycle, with 30-min simulated dawn and dusk periods. They were moved to individual cages for at least 30 min before and after the test sessions. The housing arrangements have been described at length by Dow (1984, Appendix C). Each pigeon was maintained at or over 80% of its free-feeding weight throughout the experiment by the delivery of hemp and conditioner during the experimental sessions and by supplements of mixed grain on nontesting days.

Apparatus

Two identical three-key operant chambers 690 mm by 490 mm by 390 mm were used. Each consisted of a plywood box with a 3-key intelligence panel (Campden Instruments Ltd, London), 335 mm by 350 mm, mounted centrally into the front wall. The three keys had a diameter of 25 mm and were centered 105 mm apart and 240 mm above the grid floor of the chamber. All three keys operated reed switches when struck with a force of 0.035 N. The two side keys were translucent and could be transilluminated by amber lamps. The center key was transparent, and a shutter operated by a rotary solenoid was situated behind it so that viewing a 15-inch monitor (CM1414E, Opus Technology PLC), visible 150 mm behind the center key, was prevented during the intertrial intervals (ITIs). This monitor was controlled by a PC computer (Pentium 133MHz, Opus Technology PLC) running a stimulus selection and display program written in the Borland Delphi® programming language, under the Windows 95 operating system. An aperture in the intelligence panel, 70 mm by 75 mm, was positioned 150 mm below the center key, giving access to a solenoid-operated food hopper attached outside of the box; the hopper contained a 1:2 mixture of hemp and conditioner. A 1.0-W white light within the hopper tray signaled the availability of this food. General illumination was given by a 3.5-W yellow-lensed houselight situated 120 mm above the center key. Masking noise was generated by a ventilation fan and also provided by white noise relayed by way of a 35-ohm loudspeaker mounted on the back of the intelligence panel. A separate computer was used to generate the experimental stimuli for each test chamber. Both chambers and their stimulus generation computers were housed in a darkened testing room. A further PC-compatible microcomputer (Viglen 4DX266) running under the Windows 3.1 operating system and located outside this room controlled and recorded all experimental events and responses using a program written in Borland Delphi. A network link enabled this computer to instruct the computers attached to experimental boxes in the testing room to generate the appropriate stimuli. The pigeons' behavior during experimental sessions could be regularly monitored by way of digital cameras, fitted with a wide-angle lens, mounted on the right wall of each chamber. Each pigeon was assigned to a single test chamber for all stages of the experiment.

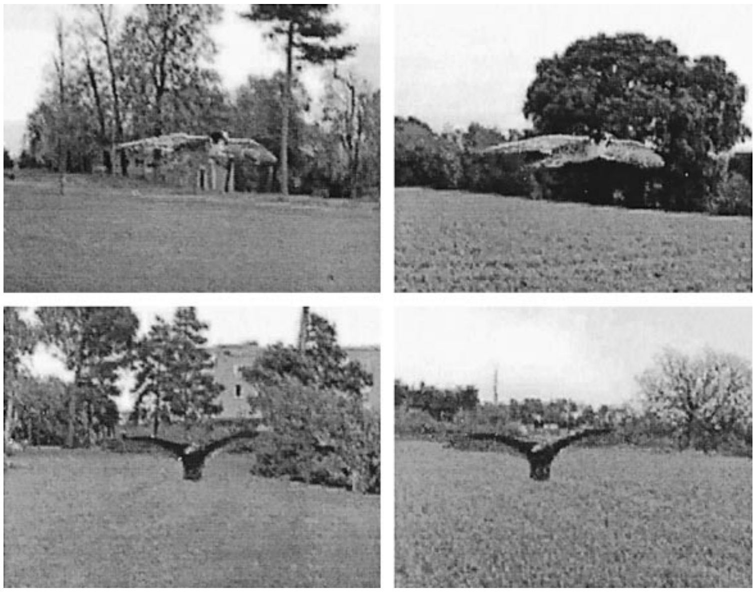

Fig. 1. Examples of frames from the movie clips used as stimuli in the experiments. In the upper panels, the bird is the peregrine (P). In the lower panels, the bird is the turkey vulture (TV). The left panels came from the Washington Singer (WS) background; the right panels came from the Garden Hills (GH) background. The movies were presented in full color.

Stimulus materials. Movie clips, and static frames from the same movies, were presented on the 15-in. (38.1-cm) computer monitor with a size of 28.5 degrees by 21.6 degrees (87 mm by 66 mm on the screen). The stationary frames were randomly chosen from the movie clips by the computers, and therefore they varied independently trial by trial.

Each stimulus was produced by the combination of a bird as a foreground and a natural scene as a background (Figure 1). Images of two flying birds were prepared by extraction from photographs found on the Internet. Two outdoor scenes of places at the University of Exeter, without any birds in view, were prepared as the backgrounds. These backgrounds were 360° panorama photographs so that a continuous loop of horizontal movement of the background could be naturally produced without discontinuity. From the combination of two birds (peregrine: P, and turkey vulture: TV) and two scenes (Washington Singer Laboratories: WS, and Garden Hills: GH), four types of movie clip were prepared under each movement condition.

Two of the stimulus sets used in the experiment involved movement of the background only, and the other two involved movement of the bird only. In addition to the varying combinations of bird and background, the selection of the background used was varied in the bird-movement sets, and the position of the birds in the stimulus was varied in the background-movement sets (further details are given below). In Set FL (Foreground moving Leftward), the bird was moved horizontally leftward against a stationary background. The location where the bird started moving was randomly chosen at every trial. When the bird left one side of the frame, it reentered the frame from the other side. In Set FR (Foreground moving Rightward), the bird was moved rightward at the same speed as in Set FL. In Set BL (Background moving Leftward), the background was moved leftward but there was no movement of the bird, and the direction of the movement of the background was reversed in set BR (Background moving Rightward). In the bird-movement stimulus sets, the bird was moved at the speed of 3.8 degrees (12 mm) per second, whereas in the background-movement sets, the background moved at the speed of 7.5 degrees (23 mm) per second. These speeds were chosen to maximize the salience

Washington Singer Laboratories

Garden Hills

Fig. 2. The complete backgrounds used in the stimuli. The movies were presented in full color.

of the movement: They were the fastest that could be used without causing the stimulus to develop a flickering effect to the human eye. Stimuli consisting of P–GH and TV–WS combinations of birds and backgrounds from Sets FL and FR were used in the training: The combinations of P–WS and TV–GH in Sets FL and FR were used in the first generalization test to examine the transfer to the same types of movement in novel combination, and those in Sets BL and BR were used in the second generalization test to examine the transfer to relative motion of foreground induced by the movement of background. Figure 2 shows the whole view of the backgrounds. They were looped continuously behind a stationary bird that was in one of five evenly spaced positions in Sets BL and BR. In Sets FL and FR, five different frames were arbitrarily chosen from each background without overlapping. All images were displayed at a size of 240 by 180 pixels. To the human eye, the motion of either the bird or the background was highly salient, and made the bird stand out very clearly from the background.

Procedure

Initial training. All the pigeons were first given magazine training, and then key pecking to the center key was manually shaped when the shutter was opened to show the monitor with a plain white screen. After the acquisition of center-key pecking, a variable-interval (VI) schedule was introduced, and the value of the mean interval was gradually raised to 10 s (range 5 to 15 s). This was then followed by training of observing key pecking, in which a peck to the illuminated left key allowed the trial to start by triggering the opening of the shutter behind the center key. Observing key training was repeated for at least three sessions to stabilize the pigeons' behavior.

Discrimination training. Following the initial training, the pigeons were trained to discriminate movement of the background or the bird from static frames extracted from the same movie files. A go/no-go schedule was used for the discrimination training. The pigeons were arbitrarily divided into two groups of 6 each, a bird-motion positive group and a background-motion positive group. Half the pigeons in each group were trained with leftward motion and the others with rightward motion. The session started with a 3-s presentation of the food hopper followed by an ITI. During the ITI, the center shutter was closed so that the pigeon could not see the computer monitor. Each trial began with the illumination of the observing key; a peck on this key eliminated its illumination then opened the shutter to reveal a stimulus on the monitor. Pecks were not reinforced during the first 10 s of each stimulus presentation (fixed time; FT). Following the completion of the FT 10 s, pecks were reinforced by a 3-s presentation of the food hopper on a VI 4-s schedule in positive stimulus trials, after which the trial ended. Negative stimulus trials terminated without the presentation of food on the expiration of a variable extinction period averaging 4 s. The trials were separated by an ITI that varied between 5 and 15 s. The sessions consisted of 80 trials that contained 4 blocks of 20 trials. Each block consisted of 10 motion and 10 stationary trials of either bird or background, presented in a pseudorandom sequence that was generated anew for each session, and constrained so that no

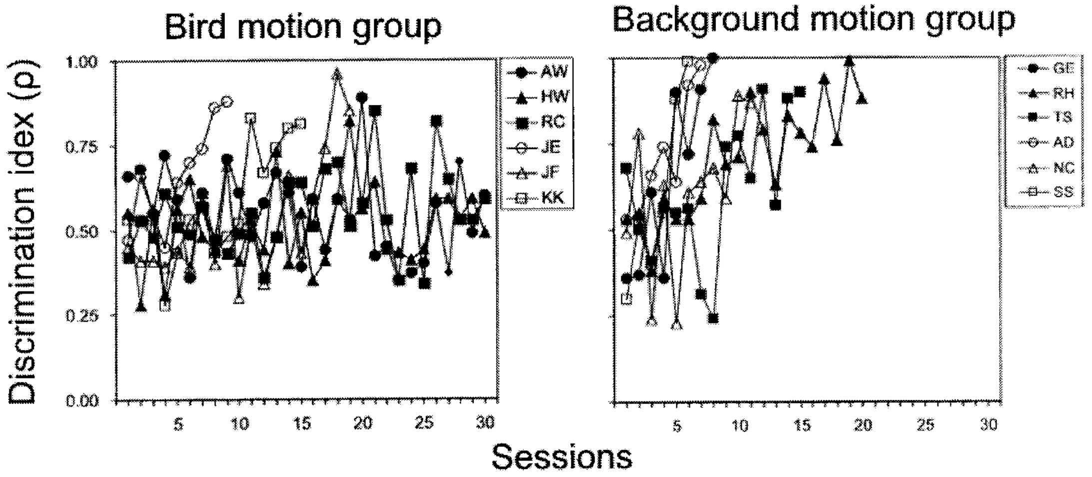

Fig. 3. Experiment 1: Acquisition of the discrimination between moving and stationary stimuli. The left panel shows acquisition in the bird-motion group, for which the positive stimulus was a bird moving against a stationary background, and the right panel shows acquisition in the background-motion group, for which the positive stimulus was a stationary bird seen against a moving background. Negative stimuli involved no motion. Pigeons JE, JF and KK in the bird-motion group and Pigeons AD, NC and SS in the background-motion group were trained with rightward motion. The other pigeons were trained with leftward motion.

more than three stimuli containing the same direction of movement were presented in succession. Sessions were given one per day, normally 6 days per week. The responses during the FT period were averaged for each stimulus, and the rho statistic of Herrnstein, Loveland, and Cable (1976) to the positive stimulus set was used as a discrimination index.

Training was continued for each pigeon until the rho statistic exceeded 0.80 in two consecutive sessions, or until 30 sessions had been completed. Once a pigeon had reached the performance criterion, generalization tests were conducted.

Generalization test. After attaining the criterion described above, the pigeons were given two generalization tests. In Test 1, novel stimulus combinations (P–WS and TV–GH) were used; these combinations of bird and background had not been used during training. The bird-movement positive group was given a single-session bird-movement test with these novel stimuli, and the background-movement groups were given a single-session background-movement test with them. The test sessions consisted of 40 positive trials, in which motion stimuli were presented, and 40 negative trials, in which stationary frames drawn from the positive stimuli were presented. Contingencies of reinforcement were maintained during these tests so that all movement trials ended with reinforcement.

In Test 2, the bird-movement positive groups were given a single-session background-movement test and vice versa. The test trials consisted of 40 positive trials, in which equal numbers of leftward and rightward movement stimuli were presented, and 40 negative trials, in which stationary frames drawn from the positive stimuli were presented. The novel stimulus combinations used in Test 1 were also used in this test, and all movement trials again ended in reinforcement. Training sessions were given between Test 1 and Test 2 until the pigeons recovered the discrimination performance, to the point where the rho statistics exceeded 0.80.

RESULTS

Figure 3 shows the acquisition of the discrimination. All 6 pigeons in the background-movement discrimination group reached the criterion, at Sessions 6, 20, 7, 8, 11, and 15. Pigeons KK, JE, and JF in the bird-movement discrimination group reached the criterion at sessions 15, 9, and 19, but the other pigeons in this group did not reach the criterion within 30 sessions. The difference in acquisition speed between the two groups is significant according to the Mann-Whitney test (U6,6 =

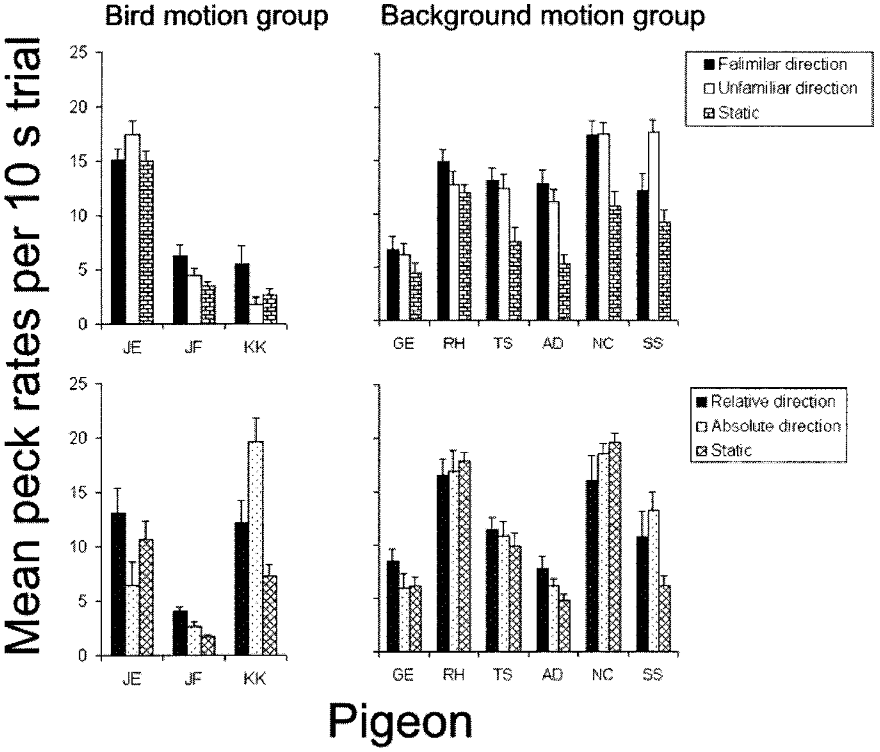

Fig. 4. Experiment 1: Results of generalization tests in the pigeons trained to peck in the presence of a stimulus including a moving bird (left panels) and a moving background (right panels). The upper left panel shows mean peck rates to the trained and untrained directions of movement of the bird, and the lower left panel shows mean peck rates to backgrounds moving in the same relative and absolute directions movement as the bird used during acquisition. The upper right panel shows mean peck rates to the trained and untrained directions of movement of the background, and the lower left panel shows mean peck rates to birds moving in the same relative and absolute directions of movement as the background used during acquisition. Error bars show standard error.

5.5, p = .043). In the bird-motion group, the 3 pigeons that reached the criterion were all trained with rightward movement, whereas the 3 pigeons that did not reach the criterion were trained with leftward movement. In the background motion group, the 2 pigeons that acquired the discrimination fastest were trained with leftward motion. These differences in acquisition speed cannot be tested for significance because of the small numbers of pigeons in each subgroup.

Figure 4 shows the result of the generalization test. Only 3 pigeons were tested in the bird-motion group because the other 3 pigeons did not reach the criterion within 30 sessions. In Test 1, Pigeon JE pecked the untrained directional motion of the novel bird more than the trained directional motion, and the difference approached significance (Mann-Whitney test, U10,10 = 27.5, p = .087), but discrimination between the trained directional motion and static frames was disrupted. The other 2 pigeons pecked the trained directional motion more than the opposite directional motion of birds, with the difference being significant in one case (KK: U10,10 = 21.5, p = .029; JF: U10,10 = 34.0, p = .221). In Test 2, Pigeons JE and JF responded to relative motion significantly more than absolute motion (JE: U10,10 = 21.5, p = .031; JF: U10,10 = 23.0, p = .037), but Pigeon KK responded to absolute motion significantly more than relative motion (U10,10 = 22.5, p = .037). In the background-motion group, Pigeon SS showed more responding to the untrained directional movement than the trained directional movement in Test 1, and the difference is significant (U10,10 = 13.5, p = .006), but the other 5 pigeons responded more to the trained movement, though the difference did not approach significance for any of them (AD: U10,10 =

43.0, *p* = .592; GE: U10,10 = 48.5, *p* = .908; NC: U10,10 = 48.5, *p* = .909; TC: U10,10 = 0.554, *p* = .544; RH: U10,10 = 36.0, *p* = .283). All pigeons, however, pecked both directions of movement more than stationary frames. In Test 2, Pigeons NC and RH did not discriminate bird motion from static stimuli; the other 4 pigeons responded more to birds moving in the untrained than the trained direction: that is, their responding appeared to be under the control of relative more than absolute motion, though the differences were not significant.

DISCUSSION

The results indicated that pigeons could indeed discriminate motion in the present stimuli. Thus, they constitute a replication of one of the results of Dittrich and Lea (1993). In addition, however, several group differences were found in this experiment.

First, the pigeons in the bird-discrimination group learned the task more slowly than the pigeons in the background-discrimination group (Figure 3). This suggests that the background movement we used was more easily discriminated by pigeons than the bird movement. Three possible factors may have contributed to making the background-movement discrimination easier than the bird-movement discrimination: the size, velocity and relative location of the moving object. The background took up more space than the bird, and therefore if size is all that matters it should have been a more salient feature than the bird. The background was moved faster than the bird in the present stimuli, and this may have made its motion easier to detect. It may also be that the perceptual location of the background cues—the mere fact that it was a background rather than a foreground—gave them stronger control over behavior. Some previous experiments have suggested that background cues are particularly important in pigeons' discrimination of pictures (e.g., Edwards & Honig, 1987), and in the present stimuli the moving background was seen against a uniform dark surround, whereas the moving bird was seen against the patterned background, which may have made the movement harder to discern.

Second, there were within-group differences in acquisition speed in terms of the direction of the movement (Figure 3). In the bird-motion group, all 3 pigeons trained with the rightward bird movement acquired the discrimination whereas the other 3 pigeons, trained with the leftward bird movement, did not reach the criterion within 30 sessions. In the background motion group, rightward motion was associated with faster learning. Although the small numbers involved preclude a test of statistical significance, the results suggest that difficulty of discrimination was associated with the relative direction of motion of the bird and background rather than the absolute direction of motion of either. The asymmetry in performance may perhaps be explained by the flying posture of the peregrine used in the stimuli. As can be seen in Figure 1, the peregrine appears to be flying rightward. To the human eye, whereas the bird looked to be moving naturally when it was moving rightward, the bird looked unnatural when it was moving leftward. This unnatural appearance might suppress the pigeons' responses to the bird moving leftward, and, as a result, the pigeons trained with those stimuli might not have been able to acquire the discrimination. Another possibility is a position bias occurring as a consequence of the observing-key responses; the pigeons always approached the center key from the right following the observing-key response. Further tests are required to confirm either of these hypotheses.

Whatever the reasons, however, it appears that the moving bird did not have the same high salience for the pigeons as it did to the human eye, and its salience may have been further reduced when it was moving in one particular direction.

EXPERIMENT 2

In Experiment 1, 9 out of 12 pigeons successfully learned to discriminate motion of either the bird or the background from stationary frames. Moreover, most of the pigeons seemed to respond more readily to movement in the training direction in generalization Test 1. This suggests that these pigeons might be able to discriminate leftward movement from rightward movement, even though the pigeons in our pilot study did not learn to do this. In the present experiment, it was assumed that the history of the motion against stationary frame discrimination in Experiment 1 might help the pigeons to learn the directional motion discrimination in a way reminiscent of the easy-to-hard task transfer effect in Lawrence (1952). Therefore, in this experiment the pigeons that had reached the criterion in Experiment 1 were used as subjects and given the task of discriminating direction of motion.

Subsequently, when the pigeons reached the criterion, they were given generalization tests that examined (a) whether they would show transfer from the trained bird-motion to the same relative or absolute direction of motion of the background and vice versa, and (b) whether they would show transfer from the trained stimuli to novel stimuli with the same type of motion as used in training. For comparison, results are also reported for the pilot study mentioned above.

METHOD

Subjects, Apparatus, and Stimulus Materials

The 9 pigeons that reached criterion in Experiment 1 were used as subjects in this experiment. Housing, maintenance, and apparatus were the same as in Experiment 1. The stimulus materials were also drawn from those used in Experiment 1, though they were associated with different contingencies of reinforcement.

In the pilot study, 12 similar pigeons were used. Housing and other conditions were identical to those reported here.

Procedure

Discrimination training. As all pigeons had already experienced a discrimination task on a successive discrimination schedule, discrimination training was started without any additional pretraining. The pigeons were trained to discriminate leftward from rightward motion of either bird or background on a go/no-go schedule. The pigeons were trained with the same part of the stimulus moving as had been used in the acquisition of phase of Experiment 1, and for each pigeon, the direction of motion that had been used during acquisition in Experiment 1 became the positive direction for this experiment. The same bird and background combinations were used in training as in Experiment 1. The training schedule was the same as in Experiment 1. Training was continued for each pigeon until the rho statistic exceeded 0.80 in two consecutive sessions, or until 30 sessions had been given. Once a pigeon reached the performance criterion, generalization tests were conducted.

The pigeons used in the pilot study were initially trained on a go left/go right conditional discrimination for 30 sessions (except for 1 pigeon that reached the criterion before this) and then for up to 30 further sessions on a schedule identical to that described here. Half of the pigeons were trained with rightward motion positive and half with leftward motion positive, and half were trained with a moving foreground and half with a moving background, in a counterbalanced manner.

Generalization tests. After attaining the criterion, that is when the rho statistic exceeded 0.80 in two successive sessions, the pigeons were given two generalization tests: (a) from sets FL, FR to sets BL, BR in the bird-movement group and vice versa in background-movement group, and (b) generalization to stimuli consisting of the familiar components but in unfamiliar combinations. Training sessions were given between tests until the discrimination performance recovered—that is, until the rho statistic again exceeded 0.80.

Figure 5 shows the acquisition of directional motion discrimination. Within the 30 sessions allowed, all 6 pigeons in the background-motion group reached the criterion, whereas only 1 of the 3 pigeons in the bird-motion group acquired the discrimination. In contrast, in the pilot study, the same discrimination task was learned by only 2 pigeons in the background-motion group and none in the bird-motion group (Figure 6). The numbers of sessions required to reach the criterion in our pilot study and in the current experiment are indicated in Table 1. In the background motion group, the pigeons in this experiment attained the criterion more quickly than the pigeons in our pilot study, and the difference was significant according to the Mann-Whitney test ($U_{6,6} = 4.0$, $p = .022$). In contrast, only 1 pigeon attained the discrimination in the bird-discrimination group even after the experience of motion-static discrimination; this is not significantly different from the results of the pilot study.

Figure 7 shows the results of generalization

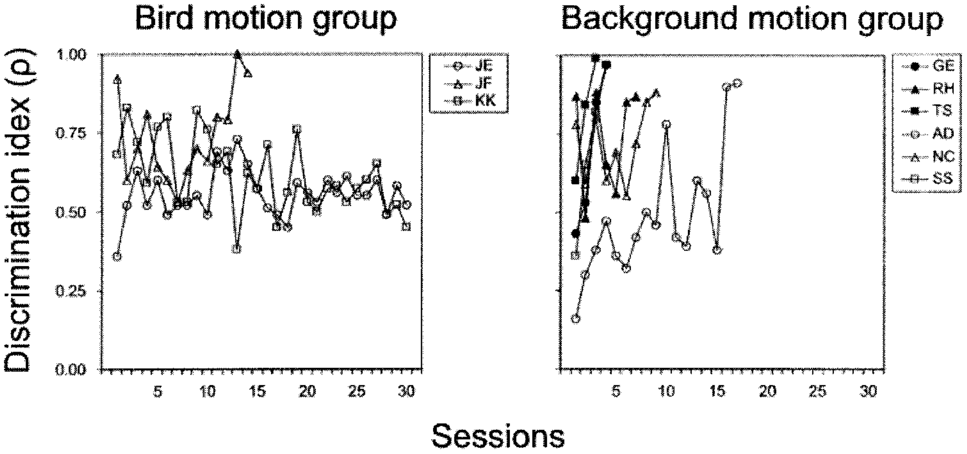

Fig. 5. Experiment 2: Acquisition of the directional motion discrimination. The upper panel shows acquisition in the bird-motion group, and the lower graph shows acquisition in the background-motion group. For all pigeons in the bird-motion group, and for Pigeons AD, NC and SS in the background-motion group, positive stimuli involved rightward motion; for the other pigeons they involved leftward motion.

tests of the successful pigeons. For each pigeon, the difference between response rates to the stimulus sets defined by the two different directional movements was examined by a Mann-Whitney test. The 1 successful pigeon in the bird-motion group showed significant transfer to motion of the background in the same absolute direction as the bird according to the Mann-Whitney test (U10,10 = 18.0, p = .015), and it also showed generalization of the trained directional discrimination to motion of novel bird/background combinations, though this effect fell short of significance (U10,10 = 27.0, p = .079). In the background motion group, Pigeon SS showed a significant tendency to peck bird-motion stimuli with the same direction of relative motion as used in training (U10,10 = 8.5, p = .002), but discriminative performance collapsed within the first 20 trials of the first test session. None of

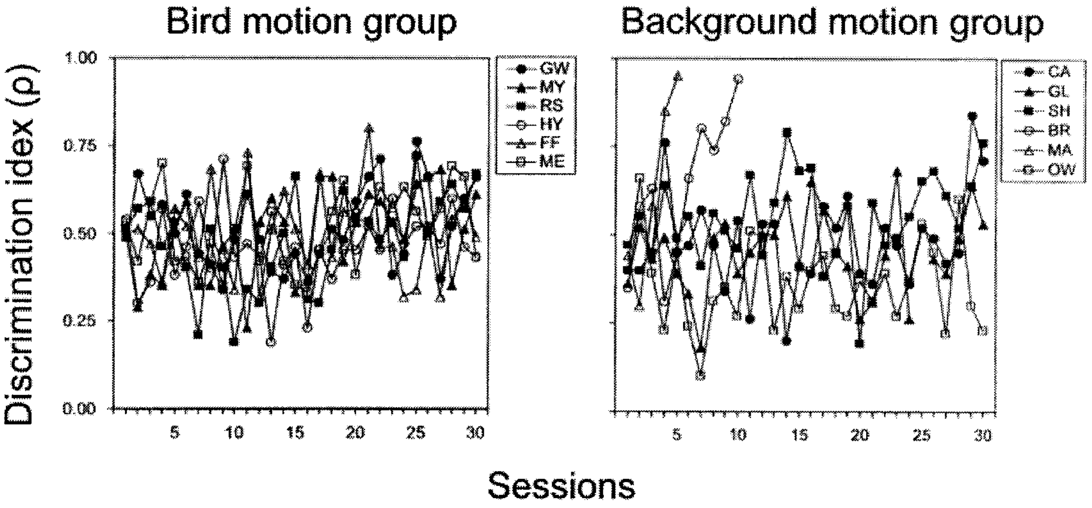

Fig. 6. Pilot experiment: Training of the directional motion discrimination. The left panel shows failure of discrimination for all pigeons the bird-motion group, and the right panel shows 2 pigeons' acquisition in the background-motion group. For Pigeons HY, FF, and ME in the bird-motion group, and for Pigeons BR, MA, and OW in the background-motion group, positive stimuli involved rightward motion; for the other pigeons they involved leftward motion.

Table 1

Number of sessions of go/no-go training. Fewer than 30 sessions were given if the criterion of discrimination was reached before this point. The pigeons in the pilot study had experienced conditional discrimination training before go/no-go training commenced; this training lasted for 30 sessions for all pigeons except the first in the table, and only this pigeon showed evidence of discrimination.

	Moving component			
	Pilot study		Experiment 2	
	Bird	Background	Bird	Background
	30	5	14	3
	30	10	30	4
	30	30	30	4
	30	30		7
	30	30		9
	30	30		17
Mean	30.0	22.5	24.7	7.3

the other pigeons showed significant differences between response rates to birds moving in the same relative and absolute directions as the background movement used in training. In Test 2, using stimuli involving novel bird/background combinations, all 6 pigeons responded more to stimuli with motion in the trained than in the untrained direction; this is a significant proportion according to a binomial test (p = .032), and for 5 of the 6 pigeons the difference was significant individually (Mann-Whitney test: SS: U10,10 = 20.0, p = .023; AD: U10,10 = 12.0, p = .004; GE: U10,10 = 8.5, p = .002; NC: U10,10 = 21.0, p = .028; TS: U10,10 = 22.5, p = .037; RH: U10,10 = 40.5, p = .909).

DISCUSSION

The results indicated that, with the present stimuli, all pigeons tested discriminated between directions of motion of the background, and that at least 1 pigeon was able to discriminate between directions of motion of the foreground bird. The difference in performance between the two groups is consistent with the greater difficulty of detection of bird movement in these present stimuli, already noted. As was discussed in connection with Experiment 1, the size, speed, or location of the foreground element may all have contributed to making it harder for the pigeons to detect bird motion than background motion in these stimuli, so it is premature to conclude that background motion as such is easier for pigeons to detect than foreground motion. It does seem clear, however, that merely moving one part of a complex scene does not necessarily give it high salience for pigeons as it does for humans.

An interesting finding of this experiment, however, is the dramatic improvement of discrimination compared with the pilot study. It seems reasonable to suggest that the experimental history of Experiment 1 influenced the pigeons' performance in the present experiment. The better performance in this experiment cannot be explained simply by longer exposure to positive stimuli for pigeons in the present study than the pigeons in our pilot study. Though the pigeons in the present study experienced two experiments with the same stimuli, the number of sessions experienced over the two experiments was less than 30 for all pigeons in the background-motion group, whereas in the pilot study almost all the pigeons were trained for a total of 60 sessions.

Generalization tests were used to confirm that responding was controlled by motion as such, rather than feature changes specific to the relative movement of a particular combination of foreground and background. In Test 2, all 7 pigeons tested showed transfer of the directional discrimination to novel combinations of bird and background stimuli when they involved movement of the same element in the same direction as in training. In Test 1, however, when the background-movement group was tested using bird rather than background movement, there was no consistency in the results: One pigeon showed significant transfer based on absolute direction of motion, one showed significant transfer based on relative direction of motion, and the others showed minimal transfer.

GENERAL DISCUSSION

Acquisition of Directional Motion

These experiments demonstrate that pigeons discriminate some patterns of directional motion without any other distinctive features. As far as we are aware, this is the first study demonstrating that pigeons are capable of discriminating motion of complex stimuli based on a single feature of the move-

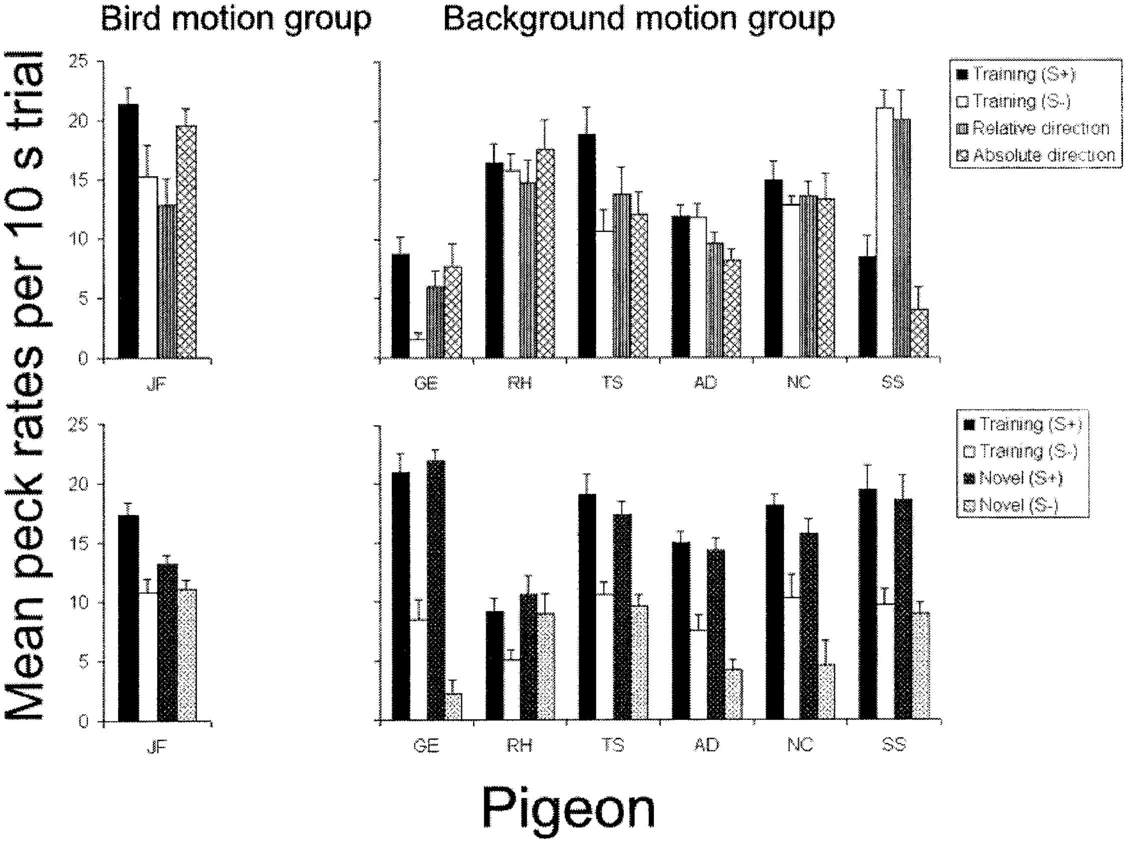

Fig. 7. Experiment 2: Generalization tests in the bird-motion group (left panels) and the background-motion group (right panels). Upper left panel: Mean peck rates to stimuli involving backgrounds moving in the positive relative or absolute direction. Lower left panel: Mean peck rates to moving-bird stimuli involving novel bird/background combinations. All pigeons were trained with rightward bird motion positive. Upper right panel: Mean peck rates to stimuli involving birds moving in the positive relative or absolute direction. Lower right panel: Mean peck rates to moving-background stimuli involving novel bird/background combinations. Pigeons AD, NC, and SS were trained with rightward background motion positive, the others with leftward motion positive. Error bars show standard errors.

ment. Previous studies have shown that pigeons are capable of discriminating complex motion patterns, but the motions could be discriminated based on the different patterns or trajectories of movement rather than a single attribute of movement (e.g. Cook, Shaw, & Blaisdell, 2001; Dittrich, Lea, Barrett, & Gurr, 1998; Emmerton, 1986).

The results, thus, demonstrate that pigeons can discriminate stimuli on the basis of their motion properties alone. No static feature could be used to discriminate the leftward and rightward motion in Experiment 2: Every static feature that appeared in the leftward movie sequence necessarily appeared equally often in the rightward sequence, because the two sequences were made up of the identical set of frames.

The discrimination of directional motion, however, was a difficult task for pigeons. In our pilot study, most of the pigeons failed to attain the criterion of discrimination, and only 1 pigeon in the bird-motion group of the present experiments attained the discrimination even after the history of Experiment 1. What, therefore, makes this kind of discrimination difficult?

First, as has just been argued, all the static features of the stimuli were exactly the same between the positive and negative sets. This did not allow pigeons to discriminate positive and negative stimulus sets, even imperfectly, based on any information in the stationary frames. Poor learning under these conditions would also be consistent with experiments showing that pigeons' acquisition of categorization of human versus nonhuman became significantly slower when other cues apart from the presence or absence of the human were well controlled than when the backgrounds were diverse (Edwards & Honig, 1987). It seems that when learning complex discriminations, pigeons often make use of cues other than those the experimenter had intended, at least in the earlier stages of learning, and forcing them to rely only on particular cues slows learning. Moreover, Jitsumori et al. (1999; Experiment 4) trained pigeons to discriminate several normally played movies of 2 different individual pigeons, and tested transfer from normal play to reversed play and static frames. The pigeons successfully transferred to reversed play without disruption and to static frames of the training stimuli, implying that in Jitsumori et al.'s experiment, motion was not the only feature used to discriminate the movies, but that the static frame contained sufficient information to support discrimination of the different movies. Randomization of the motion sequence, however, causes discrimination of normally played movies to collapse (Cook et al., 2001), which implies that the randomized sequential movies were recognized differently from the normal play movies. This combination of results suggests that the difference between directions of motion is not immediately salient for pigeons.

Second, the difficulty of the task may be related to the difficulty of mirror image discrimination. In Experiment 2, the motions of the stimuli to be discriminated were mirror images. Thomas, Klipec, and Lyons (1966) found that bimodal angularity generalization gradients, with peaks of responding at both the training stimulus and its mirror image, could be obtained by training pigeons to peck oblique lines, showing that mirror-image stimuli are spontaneously confused. It is not impossible to train pigeons to discriminate such stimuli, for Hollard and Delius (1982) reported that pigeons could learn mirror-image discriminations quickly in a simultaneous discrimination task, and the discrimination was maintained even when the images were rotated. The go/no-go discrimination procedure used in the present experiments, however, is more like Thomas et al.'s procedure than that of Hollard and Delius, so it is reasonable to conclude that it might be difficult to train pigeons to make that discrimination.

Easy-to-Hard Effect of Motion Discrimination

Although movement-direction discrimination is difficult, Experiment 2 showed that, given the right previous experience, pigeons can learn such a discrimination quickly. This improvement of performance as a function of different prior experience is similar to the easy-to-hard transfer effect (Lawrence, 1952). In his experiments, rats that experienced easier brightness discrimination showed higher discrimination performance in the harder brightness discrimination than rats with no experience of the easier discrimination. Similarly, DiPietro et al. (2002) showed that pigeons' recognition of occluded objects, often difficult to demonstrate in the laboratory, was improved by initial training on the easier task of discriminating the object from the occluder. In the present experiments, the directional discrimination was acquired more quickly by pigeons that had the history of Experiment 1 than the pigeons in the pilot study that were given directional motion discrimination immediately. Dittrich and Lea (1993) have shown that movement is readily discriminated from static scenes. Using this easy discrimination to bring behavior under the control of movement as such appears to be a potentially useful technique for training pigeons to discriminate between different kinds of complex motion.

Conclusions

The clear findings of this study are that pigeons are able to discriminate stimuli on the basis of direction of motion alone and that an experimental history of discrimination between moving and static stimuli can lead to rapid discrimination of direction of motion. The number of studies of motion discrimination in pigeons has been increasing recently (Dittrich & Lea, 2001; Lea & Dittrich, 1999). However, there has been no previous demonstration of pigeons' capability for discrimination of directional motion of naturalistic stimuli. The present research not only demonstrated pigeons' capacity to discriminate directions of motion, but also established a technique of training this difficult discrimination more successfully. The technique used here may be potentially useful for other kinds of motion discrimination study in pigeons. An experimental history of motion against static discrimination may raise the salience of many features of motion, making it easier to demonstrate pigeons' capacity to discriminate them.

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