

Recognition of moving video images of conspecifics by pigeons: Effects of individuals, static and dynamic motion cues, and movement

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Two groups of pigeons were trained with a go/no-go procedure to discriminate video images of conspecifics based on the individuals or else on their actions. Both groups showed rapid acquisition, and the discrimination transferred to new scenes in Experiment 1 and to static scenes in Experiment 2. In Experiment 3, experimentally naive pigeons were trained to discriminate video images of particular birds showing different actions. Transfer to novel scenes, including a new bird and a new motion, revealed the dominance of motion as a cue to discriminate video images. In Experiment 4, the pigeons trained to discriminate video scenes of 2 pigeons showing a variety of activities successfully recognized these stimuli regardless of whether the video was played forward or backward, and transferred the discrimination to still scenes. The findings suggest that pigeons' discrimination of video images is primarily based on information that is invariant across static and dynamic conditions.

Individual recognition is of great ecological relevance to animals. It is important for animals to respond differentially and appropriately to their social partners and to other individuals. There is little or no doubt that the ability to recognize individuals is based on perceptual and cognitive factors and on species-typical social interactive behaviors. Still or moving pictures of conspecifics have been used to study cognition and social behaviors in apes (e.g., Eddy, Gallup, & Povinelli, 1996; Menzel, Savage-Rumbaugh, & Lawson, 1985), monkeys (e.g., Plimpton, Swartz, & Rosenblum, 1981; Swartz & Rosenblum, 1980), chickens (e.g., Bradshaw & Dawkins, 1993; Evans & Marler, 1991; McQuoid & Galef, 1993; Patterson-Kane, Nicol, Foster, & Temple, 1997; Ryan, 1982), and songbird species (e.g., Adret, 1997; Brown & Dooling, 1992, 1993). The assumption has often been made that the animals perceive these stimuli as the "real" objects and scenes.

Observations of pigeons in their natural environment indicate that these birds, like most other animals, respond differentially to different individuals (Heinroth & Heinroth, 1948). Curiously, there is little or only weak evidence that pigeons are able to discriminate photographs of individual conspecifics, despite ample evidence that they are good at discriminating visual stimuli, including photographs of natural and artificial objects (see reviews in Delius & Emmerton, 1979; Emmerton & Delius, 1993;

Herrnstein, 1984; Lea & Ryan, 1990; Roitblat & von Fersen, 1992; Wasserman, 1993; Watanabe, Lea, & Ditch, 1993). Watanabe and Ito (1991) reported that pigeons discriminated slides of the heads of other pigeons. On the other hand, Ryan and Lea (1994) showed that only 1 pigeon out of 6 was successfully trained to discriminate slides of other pigeons (Experiment 1). There is evidence that pigeons clearly discriminate slides of pigeons from those of other animals (Poole & Lander, 1971), but it is not clear whether and how this species discriminates two-dimensional representations of individual conspecifics. The aim of the present study was to examine the perceptual and cognitive processes involved in pigeons' discrimination of moving video scenes of other pigeons.

Ryan and Lea (1994) attempted to find the necessary and sufficient conditions for their birds to learn a discrimination based on individual recognition. They used live pigeons (Experiment 2), moving video images of pigeons (Experiment 3), and stuffed pigeons (Experiment 4) as stimuli, and found that pigeons responded differentially only to individual live conspecifics. It is likely that these animals responded differentially to their conspecifics by relying more on dynamic actions or behaviors than static perceptual features. So far as we know, Ryan and Lea's Experiment 3 is the only published research that used moving video scenes of pigeons to study individual recognition by this species. They used a dishabituation technique that relied on pigeons' natural responses to other conspecifics as an indicator of recognition, but since the video displays did not elicit such responses, discrimination could not be explored. How animals respond to two-dimensional representations of conspecifics may relate to perceptual and cognitive ability of stimulus identification and ecological factors that may determine salience of stimulus features eliciting species-typical social responses. This find-

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ing, therefore, does not necessarily indicate that pigeons are unable to discriminate moving video images of individuals. Rather, the difficulty their birds had in discriminating stuffed pigeons when a discrimination training procedure was used (Ryan & Lea's Experiment 4) suggested that motion or dynamic activity is critical in individual recognition by these animals.

Video images may be effective in studies of individual recognition because they involve movement and motion information of stimulus animals. Pigeons are known to be able to discriminate the velocity of visual stimuli (Hodos, Smith, & Bonbright, 1975; Mulvanny, 1978; Siegel, 1970), to track moving targets (Pisacreta, 1982; Rilling & La-Claire, 1989; Wilkie, 1986), and to discriminate complex motions such as Lissajous figures (Emmerton, 1986), rotating spiral patterns (Martinoya & Delius, 1990), and images of a clock hand stimulus moving at a constant velocity (Neiworth & Rilling, 1987). The previous findings suggest that pigeons would be able to discriminate motions in video scenes. However, it is unknown whether or to what extent pigeons use motions as a cue to discriminate moving video images of other pigeons.

The video display was designed for the human eye with a particular scan rate, color mixing, and pixel density. It is not clear, therefore, whether video images depict "real" moving objects for birds. Patterson-Kane et al. (1997) suggested that, for domestic hens, video images are not adequate substitutes for real hens (see also D'Eath & Dawkins, 1996; Evans, Macedonia, & Marler, 1993; McQuoid & Galef, 1993). It is well known that the avian visual system is very different from that of humans. Many birds, including pigeons, can perceive ultraviolet light (A. T. D. Bennett & Cuthill, 1994; Emmerton & Delius, 1980; Wright, 1972a). The pigeon's retina contains more than three morphologically distinguishable cones bearing oil droplets of different color (Govardovski & Zueva, 1977) and the minima of pigeon's spectral wavelength discrimination function differ from those of humans (Blough, 1972; Jitsumori, 1978; Wright, 1972b). It has been considered that the pigeon's color vision is more than trichromatic (Jacobs, 1981), and at least pentachromatic (Delius & Emmerton, 1979). The findings in color-mixture experiments suggesting that pigeons require more than three color components to match another wavelength (Jitsumori, 1976) seem to agree with this conclusion. The color video images that are adequately realistic for humans are, therefore, most likely chromatically false for birds.

We do not know what pigeons tend to see in moving video scenes of other pigeons, but there is little or no doubt that video images present information of complex shape of object and its motion. Experiment 1 examined whether pigeons utilize these different types of information to discriminate video images of other pigeons. One group was trained to discriminate video scenes of moving pigeons based on individuals, and the other group was trained to discriminate these stimuli based on motions. They were then tested for transfer to new scenes (generalization tests in Experiment 1) and to sta-

tic scenes (Experiment 2). A moving image may provide information that is not available in a single static picture or the corresponding set of moment-to-moment still images, but humans are often able to abstract the activity of another person from a mere snapshot. We can recognize, for example, a snapshot of a person walking, dancing, eating, or engaging in other activities. On the basis of the finding of Experiment 2 that pigeons readily generalized from dynamic to static scenes, two experiments were designed to examine the extent to which motions (Experiment 3) and movement itself (Experiment 4) were used to recognize video scenes of individuals showing different activities.

EXPERIMENT 1

The question addressed in the first experiment was whether pigeons would discriminate moving video scenes of conspecifics based on the individuals or their motions. The stimuli were video recordings of object birds displaying particular responses manually shaped in the experimental chamber in which subject birds were later tested. Four pigeons were trained to discriminate the individuals showing the same motion (the bird discrimination group), and an additional 4 pigeons were trained to discriminate the motions of an individual (the response discrimination group). Note that because motion inevitably involves information regarding a bird and its response, we have referred to the latter group as "response discrimination" rather than "motion discrimination" to clarify the task requirements. After completion of the training, the pigeons were tested for transfer to new scenes. The test scenes involved new object birds for the response discrimination group and new motions for the bird discrimination group, respectively.

Method

Subjects

Eight experimentally naive homing pigeons of retired racing stock were randomly allocated in equal numbers to the two groups at the start of the experiment. They were maintained at 80%–85% of their free-feeding weights throughout the experiment. The birds were caged individually in an outdoor aviary on a roof of the department building. Water and grit were freely available in the home cages. Sessions were conducted during the daytime, from approximately 10:00 a.m. to 5:00 p.m.

Apparatus

The videos were displayed via a videodisk player (Sony LVA3700) on the 14-in. screen of a color monitor (Sony PVM1454Q) positioned 2 cm in front of the experimental chamber (35 × 35 × 38 cm). The pigeons could view the screen through a transparent rectangular key (screen key), 11 cm high and 13 cm wide. The screen key was positioned 11 cm above the floor on the front wall of the operant chamber. A 1.5- × 4.0-cm food aperture, located on the floor and centered below the screen key, gave 3-sec access to a solenoid-operated food tray (Sanso Floor-type CD-1) containing a mixture of food grains. When food was available and the food tray was presented, a small lightbulb (2W) immediately below the aperture turned on. A 2-cm-diameter key (start key) was on the rear wall of the chamber. It was centered on the wall 19 cm above the floor.

The start key allowed the pigeons to initiate trials and to see the video display at different distances while they were approaching the screen key. A houselight (3W) placed at the center of the ceiling dimly illuminated the chamber. The chamber and the video monitor were in a darkened testing room. A micro computer system (NEC-9821) selected an appropriate starting frame on a videodisk (Sony LVM3AA0) in each trial, controlled experimental events, and collected responses.

Stimulus Materials

Video recordings were made of 3 male object birds. They were gray pigeons of slightly different sizes and shades of gray. The object birds were referred to as Objects A, B, and C. In the experimental chamber, three different responses were manually shaped in the object birds; key pecking (pecking the screen key), circling (circling in the chamber), and pacing (pacing up and down the chamber on the side nearest the observer, showing frontal view with the neck raised and the head moving to the left and to the right). Lighting was provided by overhead fluorescent lights. The object bird was recorded in color with the video camera (Sony CCD-VX1), with the outer boundaries of the chamber forming the edges of the picture. The scene was filmed for about 1 h and then edited on a videodisk recorder (Sony LVR-3000) to make up a 5-min scene of the object bird continually repeating a given behavior. Excerpts from the 5-min scene were presented as stimuli. The video frames did not overlap between the excerpts. The duration of the excerpts used for training was 20 sec on average, but depended on a predetermined sequence of scheduled trial intervals. Six different sequences were used in random order. The duration of the excerpts used for the test was 10 sec. The excerpts from a given scene appeared, as nearly as possible, equally often across sessions in each experimental phase. Video scenes of Objects A, B, and C each showing key pecking, circling, and pacing were prepared. The scenes that were not used in Experiment 1 were used in the later experiments.

Procedure

Preliminary training. The subject pigeons were first trained to peck on the screen key, using a conventional hand-shaping procedure. As soon as they were pecking consistently, the number of pecks required was gradually increased to 30 (fixed ratio 30), and at least three sessions were given in which 60 reinforcers were provided. During this phase, the video monitor displayed a white unpatterned stimulus. The pigeons were then trained to peck on the start key and at least three sessions were given on a schedule of continuous reinforcement. In the final phase of preliminary training, the pigeons were given 60-trial sessions, with an intertrial interval of 5 sec during which the houselight turned on and a blank frame was displayed on the monitor. At the start of each trial, only the start key was illuminated. A single response on the start key turned it off and a white unpatterned stimulus was then presented on the video monitor. Thirty pecks on the screen key produced food delivery. This training phase, which was included to ensure that the pigeons moved to the screen key immediately after they had pecked on the start key, lasted at least three sessions.

Experimental procedure. The response discrimination group (Birds 1, 2, 3, and 4) were trained to discriminate the video scenes of Object A showing two different motions, circling and key pecking. The positive motion was circling and the negative motion was key pecking for Birds 1 and 2, and vice versa for Birds 3 and 4. The bird discrimination group (Birds 5, 6, 7, and 8) received training with the video scenes of Objects A and B showing the same motion, circling. Object A was positive and Object B was negative for Birds 5 and 6, and vice versa for Birds 7 and 8.

The pigeons were trained to discriminate video scenes on a go/no-go discrimination task similar to that used by Vaughan and

Greene (1984). The pigeons started trials by pecking once on the start key as in the final phase of preliminary training. A session consisted of 30 positive and 30 negative trials in pseudorandom order with the restriction that no more than three positive or negative trials could occur in succession. For the first 10 sec after the video scene was displayed on the monitor, pecks on the screen key were recorded but had no further consequence. Following this 10-sec period, a variable interval (VI) 8-sec component started. On positive trials, a peck after the end of a scheduled interval was reinforced. On negative trials, pecks were not reinforced. A negative trial terminated after a scheduled interval on the VI 8 sec had expired and 5 sec had passed without responding. When a trial did not terminate within 2 sec after the scheduled interval had expired, the videodisk player continually repeated the same excerpt. The video image was broken for a brief moment when the videodisk player went back to the first frame for that trial. This occurred only at the beginning of training when the pigeons continued to respond on negative trials. The number of responses during the first 10 sec was used to calculate response rate. Training continued until 90% or more of the total responses occurred in positive trials in each of two consecutive daily sessions.

After having attained the criterion, the pigeons received Test 1. A session consisted of 30 training trials (15 positive and 15 negative) and 30 test trials. In test trials, 10-sec excerpts from two new scenes were presented equally frequently. The new scenes were those showing a new object bird (Object B) in the positive and negative motions for the response discrimination group, and those showing Objects A and B in a new motion (key pecking) for the bird discrimination group, respectively. Four test sessions were given.

After completion of Test 1, the pigeons received training with the four scenes that had appeared during Test 1 (a set of the positive and negative scenes used in the initial training phase and a new set of positive and negative scenes used for the test). Training continued until the 90% criterion was attained with each set of the positive and negative scenes in each of two consecutive daily sessions. After having attained the criterion, the pigeons received Test 2. A session consisted of 30 training trials and 30 test trials. Across four test sessions, the four scenes used in the preceding training phase appeared equally frequently on training trials. The new scenes presented on test trials were those involving a new object bird (Object C) showing the positive and negative motions for the response discrimination group, and Objects A and B showing a new motion (pacing) for the bird discrimination group, respectively. Other procedural details were the same as in Test 1.

Results

The pigeons in both groups showed rapid acquisition. The mean number of sessions required to reach the acquisition criterion was 9.8 (range, 7–13) for the response discrimination group and 9.3 (range, 6–14) for the bird discrimination group. In Test 1, the pigeons in the response discrimination group were tested for transfer to a new object bird (Object B) and those in the bird discrimination group were tested for transfer to a new motion (key pecking). The left panel of Figure 1 shows response rates (responses/minute) on training and test trials for the response discrimination group. The left panel of Figure 2 shows the results for the bird discrimination group. Except for Bird 4, the pigeons in the response discrimination group showed higher response rates to the new positive stimuli than to the new negative stimuli. The pigeons in the bird discrimination group showed a similar tendency,

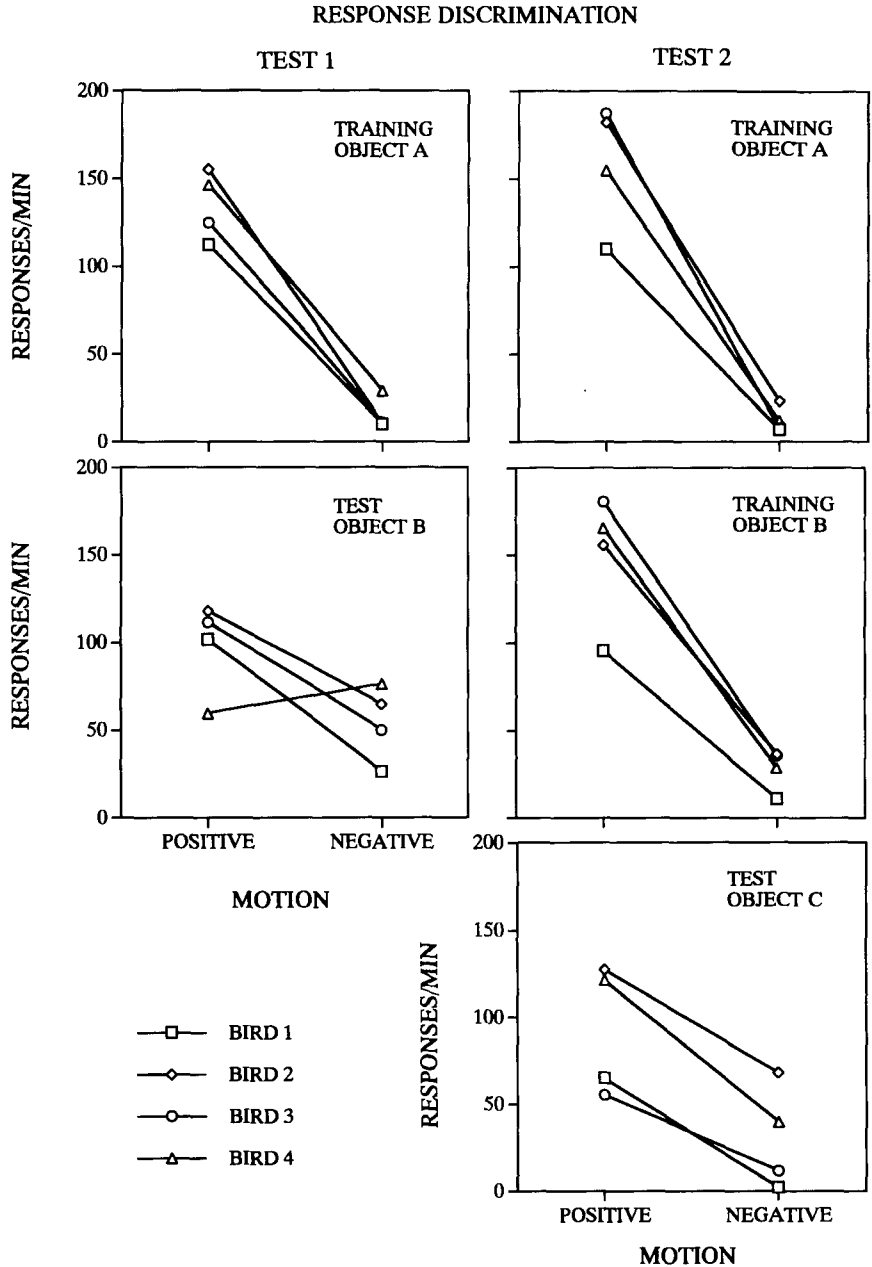


Figure 1. Response rates in responses per minute for training and test stimuli in Experiment 1, Test 1 (left panel) and Test 2 (right panel) in the response discrimination group.

but responding to the new positive stimuli was decreased substantially on test trials. A repeated measures, two-way analysis of variance (ANOVA), with relevant feature (positive vs. negative) and trial (training vs. test) as variables, was separately conducted for the response discrimination and bird discrimination groups. In this and all other statistical tests, an alpha level of .05 was used. A significant main effect was found for relevant feature for both the response discrimination group [$F(1,3) = 58.22$] and the bird discrimination group [$F(1,3) = 16.6$]. The effect of trial

was not significant. The interaction was significant in the response discrimination group [$F(1,3) = 10.65$] and in the bird discrimination group [$F(1,3) = 11.07$]. The interaction reflects the finding that discrimination of the positive and negative stimuli deteriorated on test trials relative to training trials, due to the novelty of the stimuli and/or the extinction procedure. A contrast analysis revealed marginal differences between response rates to the new positive and negative stimuli only in the response discrimination group [$F(1,3) = 6.83, p = .08$].

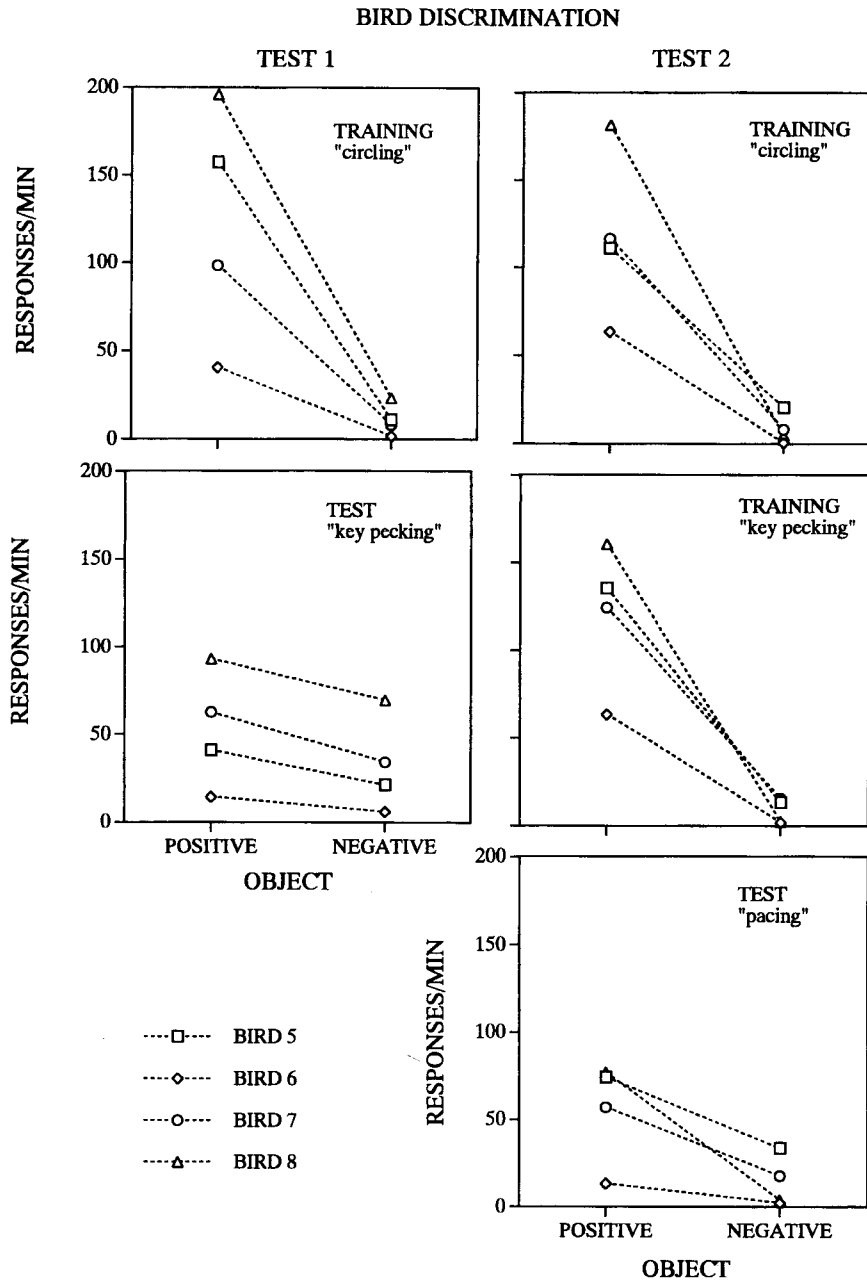


Figure 2. Response rates in responses per minute for training and test stimuli in Experiment 1, Test 1 (left panel) and Test 2 (right panel) in the bird discrimination group.

In Test 2, the pigeons in the response discrimination group were tested for transfer to a new object bird (Object C) and those in the bird discrimination group were tested for transfer to a new motion (pacing). The right panel of Figure 1 shows response rates on training and test trials for the response discrimination group. The right panel of Figure 2 shows those data for the bird discrimination group. All the pigeons showed higher response rates to the new positive stimuli than to the new negative stimuli (see the bottom-right graphs of Figures 1 and 2). A

repeated measures, two-way ANOVA revealed a significant main effect of relevant feature (positive vs. negative) in the response discrimination group [$F(1,3) = 146.21$] and in the bird discrimination group [$F(1,3) = 22.61$]. The effect of scene (Object A on training trials vs. Object B on training trials vs. Object C on test trials in the response discrimination group; circling on training trials vs. key pecking on training trials vs. pacing on test trials in the bird discrimination group) was not significant. The interaction was significant in the response discrimination group

[$F(2,6) = 14.56$] and in the bird discrimination group [$F(2,6) = 30.93$]. A contrast analysis revealed that the differences between response rates to the new positive and negative stimuli were significant in the response discrimination group [$F(1,6) = 29.79$] and in the bird discrimination group [$F(1,6) = 31.37$]. Although the discrimination more or less deteriorated on test trials, the pigeons in both groups eventually showed transfer to the new stimuli in Test 2.

Discussion

The pigeons in the response discrimination group and the bird discrimination group were successfully trained to discriminate the video scenes. The rapid acquisition in both groups suggests that pigeons are capable of learning discrimination of moving images of other pigeons on the basis of either the motion or the object, depending on task requirement. In Test 1, the pigeons in both groups showed slightly higher response rates to the new positive stimuli than to the new negative stimuli (the one exception was Bird 4 in the response discrimination group). However, the discrimination was not statistically significant. The discrimination eventually transferred fairly well to the new stimuli in Test 2.

Dittrich and Lea (1993) found that pigeons could respond discriminatively to moving and static video images of objects, including pigeons, humans, other animals, parts of a tree, and computer-generated geometrical shapes. They interpreted this as the formation of a "motion" concept by pigeons. In contrast, the present finding in the response discrimination group demonstrated that motions of different kinds controlled pigeons' discriminative performance. Although the discrimination performance more or less dropped with the scenes of new object birds under extinction conditions, we may conclude that pigeons are capable of abstracting information of motions from video images of moving pigeons. In the bird discrimination group, on the other hand, rates of responding to the positive bird in new motion were substantially decreased on test trials. It is highly likely that the new motion changed the images of individual birds in shape, size, and position on the video screen. However, the pigeons still discriminated the positive and negative birds. The present experiment was not designed to directly explore the physical dimensions of stimuli, or features, underlying recognition of video images of individuals. The findings in this group suggest that pigeons are capable of learning individual recognition that is invariant with respect to specific types of movement or the motions shown by individuals.

EXPERIMENT 2

The moving video displays used in Experiment 1 were lacking three-dimensionality and natural color, and were not life-size images, all of which features were offered by the stuffed pigeons used by Ryan and Lea (1994). Nevertheless, the bird discrimination group was successfully

trained to discriminate moving images of individuals, whereas Ryan and Lea failed to train their pigeons to discriminate stuffed pigeons. This suggests that movement is critical for pigeons to learn individual recognition. Experiment 2 assessed the contribution of movement for pigeons to recognize scenes of other pigeons. More specifically, the pigeons in both groups were tested for transfer to still scenes.

The still scenes consisted of frozen frames from the moving scenes used for training. Because movement is usually important for recognizing activity patterns, we expected that discriminative performance would severely deteriorate when static scenes were presented to the response discrimination group. On the other hand, because perceptual features of individuals could be retained in static scenes to some extent, we expected that the pigeons in the bird discrimination group might be able to discriminate the static scenes. If, however, the absence of movement were to disrupt the performance of the pigeons in this group, we could conclude that pigeons do not rely much on static features in individual recognition, which would confirm previous biological studies (M. A. Bennett, 1939; Craig, 1908, cited in Ryan & Lea, 1994; Whitman, 1919).

Method

Subjects and Apparatus

The subjects were 8 pigeons tested in Experiment 1 (Birds 1–8). Housing, maintenance, and apparatus were as in Experiment 1.

Stimulus Materials

The moving scenes were the same as those used in Test 2 of Experiment 1. Twenty frozen frames were pseudorandomly selected from each of the six moving scenes so that they could depict a variety of separate instances of activity, for a total of 120 static scenes.

Procedure

The pigeons were trained with the six moving scenes (three sets of the positive and negative scenes) used in Test 2 of Experiment 1, until they attained the 90% criterion for each set in each of two consecutive daily sessions. They were then tested with static scenes. Two test sessions were given, each consisting of 60 test trials. The stimulus duration was 10 sec, and each still scene appeared once during the test. Test sessions were given in extinction (no rewards and no penalties). Other procedural details were the same as in Experiment 1.

Results

The mean number of sessions required to regain the acquisition criterion was 20.0 (range, 11–28) for the response discrimination group and 21.8 (range, 10–37) for the bird discrimination group. Although the pigeons showed high accuracy of discrimination at the beginning of retraining, further training sessions were required for the pigeons to attain the 90% criterion on two consecutive sessions with each of the three sets of positive and negative scenes.

The left panel of Figure 3 shows response rates to the positive and negative static stimuli in the response discrimination group and the right panel shows these results

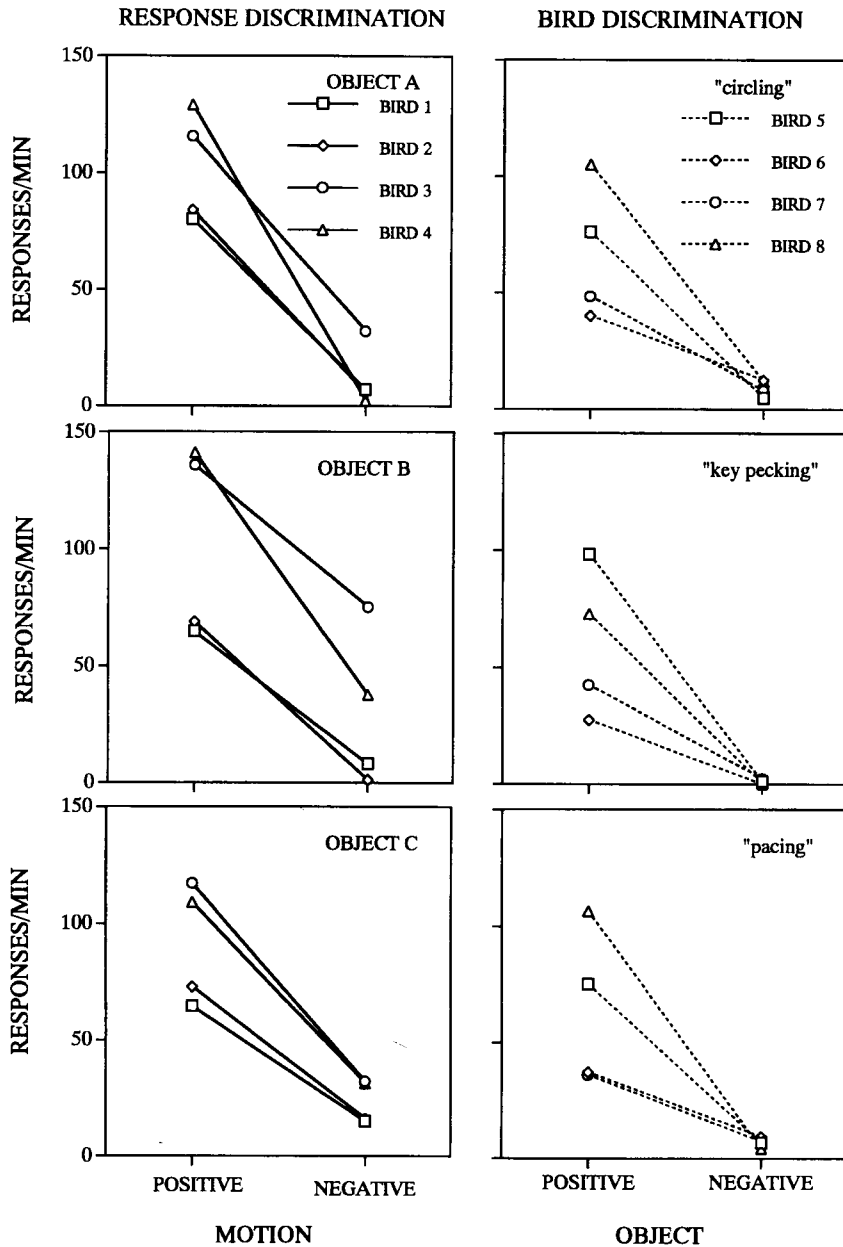


Figure 3. Response rates in responses per minute for the static scenes tested in Experiment 2.

in the bird discrimination group. Bird 6 ceased responding in the second test session, and data from only the first test session were used for analysis in this bird. The static stimuli substantially decreased overall rates of responding, whereas all the pigeons responded at higher rates to the positive stimuli than to the negative ones. A repeated measures, two-way ANOVA, with relevant feature (positive vs. negative) and scene (Object A vs. Object B vs. Object C for the response discrimination group, circling vs. key pecking vs. pacing for the bird discrimination group) as variables, revealed a significant effect only for

relevant feature in the response discrimination group [$F(1,3) = 67.93$] and in the bird discrimination group [$F(1,3) = 14.41$]. Thus, the pigeons transferred the discrimination of moving scenes to the corresponding still scenes.

Discussion

The pigeons in both groups discriminated the static scenes correctly. That is, the motion discrimination as well as the object discrimination learned by the pigeons with moving scenes readily transferred to the correspond-

ing still scenes. This finding strongly suggests that movement itself is not critical for pigeons to recognize known video images. Rather, visual information that is specific to particular scenes, no matter whether they are moving or static, is critical.

The pigeons in the response discrimination group were trained to discriminate circling and key pecking of the object birds. The still scenes of circling included a wide variety of images of the object bird in side, frontal, and rear views, with the head in various positions. In contrast, the still scenes of key pecking contained images of the object bird only in a side view showing its right profile with the bill directed toward the key, and were relatively similar to one another (at least for human observers). Training with these two particular motions might have promoted the pigeons' transfer to the discrimination of the corresponding still scenes. It is apparent, however, that the static scenes were recognized as versions of, or at least not distinctly different from, the original moving scene for pigeons.

Ryan and Lea (1994) reported difficulty in training pigeons to discriminate slides of other pigeons (Experiment 1). The present finding in the bird discrimination group indicates that, once pigeons had learned to discriminate moving images of other individuals, they could readily recognize the known individuals in static scenes, a finding suggesting considerable cognitive plasticity in pigeons. This issue is discussed later in the General Discussion section.

EXPERIMENT 3

The findings from Experiment 2 suggest that information of particular scenes, regardless of the presence and absence of movement, is sufficient for pigeons to recognize known scenes. It appears that the motion discrimination was based not on movement feature but on visual information of particular scenes that could be retained in the corresponding still scenes. Such information could be determined by visual features of particular individuals and their motions. In Experiment 1, the response discrimination group showed better transfer to new scenes than the bird discrimination group; the new motions substantially deteriorated discrimination of the positive and negative birds in the bird discrimination group. It is highly likely that motions of different kinds rather than individuals would more largely change information of particular scenes. We expected, therefore, that motions rather than individuals would more powerfully control discrimination of video scenes when these different types of information are both available for pigeons to discriminate the stimuli. An opposite prediction may also be tenable, if one assumes that pigeons would readily abstract information of individuals that is invariant with respect to the moment-to-moment change of dynamic scenes.

To determine the extent to which individual birds and their motions exercised differential control, experimentally naive pigeons were trained to discriminate moving video images of 2 birds showing different motions. The positive

scene involved a positive bird showing positive motion (bird+/motion+), and the negative scene involved a negative bird showing negative motion (bird-/motion-). Thus, the object and/or the motion enabled the pigeons to discriminate the stimuli. After training, the pigeons were tested for transfer to novel scenes showing the positive bird in negative motion (bird+/motion-), the negative bird in positive motion (bird-/motion+), a new bird in positive motion (new/motion+), a new bird in negative motion (new/motion-), the positive bird in new motion (bird+/new), and the negative bird in new motion (bird-/new). Comparisons of their performances to the novel stimuli would allow us to differentiate discrimination on the basis of individuals from discrimination on the basis of motions.

Method

Subjects, Apparatus, and Stimulus Materials

Five experimentally naive homing pigeons served as subjects. Housing, maintenance, apparatus, and stimulus materials were as in Experiments 1 and 2.

Procedure

The positive scene (bird+/motion+) was Object A showing circling and the negative scene (bird-/motion-) was Object B showing key pecking for Birds 9-11, and vice versa for Birds 12 and 13. Training continued until 90% or more of the total responses occurred in positive trials in each of two consecutive daily sessions. Other procedural details were the same as in Experiment 1.

After completion of the training, the pigeons were tested for transfer to novel scenes: the bird+/motion-, bird-/motion+, new/motion+, new/motion-, bird+/new, and bird-/new scenes. The new bird was Object C and the new motion was pacing. Six test sessions were given. A session consisted of five randomized blocks of 12 trials. Within a block, there were three positive and three negative training trials and six test trials (each of the six novel scenes was presented once). Test trials lasted for 10 sec, and responses were not followed by either reward or penalty. Other procedural details were the same as in the training sessions.

Results

All pigeons showed rapid acquisition and reached the criterion level within 14 sessions. The mean response rates to the positive and negative stimuli in the last two sessions of training were 72.6 and 6.4 for Bird 9, 89.9 and 9.2 for Bird 10, 188.3 and 1.4 for Bird 11, 174.3 and 5.3 for Bird 12, and 169.2 and 6.8 for Bird 13, respectively.

Table 1 shows response rates for each of the test and training stimuli in test sessions. Although pigeons' pecking rate dropped substantially in the presence of novel stimuli tested in extinction, systematic differences can be seen in the rate of responding to the test stimuli. A one-way ANOVA, with test scene as a within-subjects variable, revealed a significant effect [$F(5,20) = 5.91$]. A contrast analysis was conducted between the bird-/motion+ and bird+/motion- scenes, the new/motion+ and new/motion- scenes, and the bird+/new and bird-/new scenes. A significant difference in rate of responding was found between the bird-/motion+ and bird+/motion- scenes and between the new/motion+ and new/motion- scenes.

Table 1
Response Rates (Responses/Min) to the Training and Test Scenes in Experiment 3

Subject	Training		Test	
	Bird+/Motion+	Bird-/Motion+	New/Motion+	Bird+/New
Bird 9	63.1	42.2	22.6	47.6
Bird 10	89.5	62.6	39.7	69.2
Bird 11	142.1	44.2	39.2	55.6
Bird 12	157.9	53.0	51.0	11.4
Bird 13	153.7	109.6	64.6	20.2
Mean	121.3	62.3	43.4	40.8
Subject	Bird-/Motion-	Bird+/Motion-	New/Motion-	Bird-/New
Bird 9	5.0	3.6	12.6	13.8
Bird 10	7.4	22.0	17.7	27.6
Bird 11	0.3	4.4	13.8	34.8
Bird 12	1.2	18.0	13.6	10.4
Bird 13	1.6	40.6	28.6	34.2
Mean	3.1	17.7	17.3	24.2

Note—bird+, positive bird; bird-, negative bird; new/, new bird; motion+, positive motion; motion-, negative motion; /new, new motion

Figure 4 compares response rates averaged across the 5 pigeons. As shown in the left panel, the type of motion more powerfully controlled responding than the individual birds; the pigeons pecked more often at the bird-/motion+ scene than the bird+/motion- scene. The middle panel shows response rates to the new/motion+ and new/motion- scenes. When the scenes involved the new bird, the pigeons tended to show a higher rate of responding to the positive motion than to the negative one. A similar, but less manifest, tendency can be seen in the right panel; the positive bird controlled higher response rate than the negative bird when both were in the new motion. Thus, the motion cue and the object cue were both used by the pigeons to discriminate the new scenes, but the motion cue was more salient than the object cue. However, comparisons across the 5 pigeons in Table 1 revealed that only Birds 9-11 showed a clear difference between key pecking to the positive and negative birds showing the

new motion. In Birds 12 and 13, pecking rates to the positive bird dropped substantially in the presence of this motion. The new motion might have overshadowed the object cue for these pigeons to discriminate the new scenes. This is discussed later.

Discussion

Pigeons were successfully trained to discriminate video scenes of 2 particular birds showing different motions. On the basis of the findings of Experiments 1 and 2, we expected that the motion cue would more powerfully control responding than the object cue. Performances to the new scenes supported this position. Higher rates of responding to the bird-/motion+ scenes than to the bird+/motion- scene clearly indicated the dominance of motion. The discrimination based on the motion was evident for the scenes involving the new bird, while control by the object birds was not impressive with the scenes involving the new

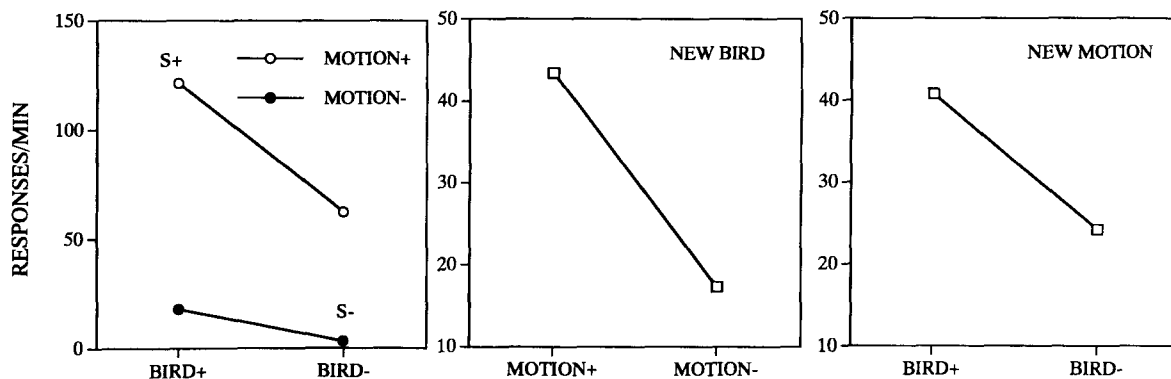


Figure 4. Response rates in responses per minute for the training scenes and the bird+/motion- and bird-/motion+ scenes (left panel), the new/motion+ and new/motion- scenes (middle panel), and the bird+/new and bird-/new scenes (right panel) in Experiment 3. In the left panel, S+ represents the positive training scene, and S- represents the negative training scene.

Table 2
Response Rates (Responses/Min) to the Positive
and Negative Scenes in Experiment 4

Bird	Test 1				Test 2	
	Training Trials		Test Trials		Static Scenes	
	Positive	Negative	Positive	Negative	Positive	Negative
Bird 9	81.8	12.8	63.8	4.8	40.0	10.5
Bird 10	34.4	7.0	36.2	6.4	60.3	23.9
Bird 11	73.0	7.6	82.8	12.4	83.8	21.6
Bird 12	196.6	33.0	183.0	16.6	126.6	19.4
Bird 13	144.0	3.4	139.2	7.4	75.2	13.1
Mean	106.0	12.8	101.0	9.5	77.2	17.7

motion. Birds 12 and 13 showed equally low rates of responding to the positive and negative birds when both showed the new motion (pacing). These 2 pigeons received training with key pecking as the positive motion and circling as the negative one. The negative and new motions involved bodily locomotion of the object bird, while the positive motion did not. It is likely that the bodily locomotion of pacing induced these 2 pigeons to refrain from pecking, regardless of whether the object bird was positive or negative. All in all, the findings indicated the dominance of motion as a cue to discriminate moving images of other pigeons.

EXPERIMENT 4

The findings of Experiments 2 and 3 suggested that, although motion is highly salient for pigeons, movement of conspecifics is not important for them to discriminate video images. In these experiments, the pigeons were shown moving video scenes of individuals continually repeating a given action. These stimuli may have promoted the pigeons to respond relying on information of particular motion scenes that was common to both the moving and the corresponding still scenes. In Experiment 4, video scenes of 2 pigeons, each showing a variety of activities in a natural setting, were used as stimuli. One scene was played in the normal direction and the other one was played in the reversed direction during training. Thus, information of a particular scene and the play direction (ecologically valid or invalid movement) were both available for pigeons to recognize the stimuli. Given a wide variety of motions of individual birds, pigeons probably do not respond on the basis of information of particular motion scenes; it would be more economical for pigeons to discriminate the stimuli on the basis of the movements. Test 1 examined the extent to which these different types of information were used to recognize the video images. In Test 2, generalization to still scenes was tested to assess the generality of the finding of Experiment 2.

Method

Subjects and Apparatus

The subjects were 5 pigeons tested in Experiment 3 (Birds 9–13). Housing, maintenance, and apparatus were as in Experiment 3.

Stimulus Materials

Video scenes of 2 different domestic pigeons visiting the roof of the department building were prepared. One scene (Scene 1) involved a pigeon walking to the left and right, standing still while moving its head in various ways, and bowing. The other one (Scene 2) involved another pigeon walking or running to search for food, pecking on the floor, and turning on the spot. The background was identical and consisted of the rooftop floor and a fence. The duration of each scene was 32 sec. Thirty frozen frames were pseudorandomly selected from each scene so that they would include a wide variety of postures of the object bird.

Procedure

The positive scene was Scene 1 played in the normal direction and the negative scene was Scene 2 played in the reversed direction for Birds 9–11, and vice versa for Birds 12 and 13. Thus, the particular scene and/or the play direction (ecologically valid or invalid movement) enabled the pigeons to discriminate the stimuli. A session consisted of 30 positive and 30 negative trials. If a trial did not terminate until the 32-sec scene had ended, the same scene was continually repeated. Other procedural details were the same as in training sessions in Experiment 3.

After the pigeons reached the 90% criterion, they were given four test sessions in Test 1. A session consisted of 30 training trials (15 positive and 15 negative) and 30 test trials. In test trials, the scene was played in the opposite direction relative to that in training trials; the scene originally played in the normal direction was played in the reversed direction, and vice versa. Other procedural details were the same as in test sessions in Experiment 3. After completion of Test 1, the pigeons received retraining sessions until the 90% criterion was regained. They were then given Test 2, in which each of the 60 static scenes (30 from Scene 1 and 30 from Scene 2) was presented once in a session of 60 test trials. Two test sessions were given in extinction. Other procedural details were the same as in the test sessions of Experiment 2.

Results and Discussion

The sessions required to reach the acquisition criterion were 12, 13, 26, 11, and 12 for Birds 9–13, respectively. The rates of responding to the positive and negative scenes in Test 1 are shown in the left-hand columns of Table 2. We expected that the pigeons would use the movement type as a cue to discriminate the stimuli, but this was not the case. The scene discrimination was maintained even when each moving scene was played in the opposite direction in test trials. Thus, the pigeons discriminated the moving scenes regardless of whether the movement was ecologically valid or invalid. Because the task requirement

did not require the pigeons to abstract the ecologically valid and invalid movements, we cannot conclude that pigeons are unable to discriminate the movement types. It is clear, however, that information about the particular scenes rather than the play direction predominantly controlled the discriminative performance of the pigeons.

The rates of responding to the static scenes in Test 2 are shown in the right-hand columns of Table 2. All the pigeons showed higher rates of responding to the positive still scenes than to the negative ones. Thus, the pigeons readily generalized from the dynamic to the static scenes, a finding in agreement with that of Experiment 2. The present experiment was not designed to assess differential control by individuals and their motions. However, it seems unlikely that the pigeons responded relying on specific features of individual birds that were invariant with respect to the moment-to-moment change of the dynamic scenes. The different kinds of motions rather than individuals would more largely change information of particular scenes, since it was revealed in Experiment 3 that these pigeons showed the dominance of motion as a cue to discriminate moving scenes of particular pigeons. Information of particular motion scenes that is common to both the static and dynamic scenes and to the different types of movements might have predominantly controlled their responding. Given the capacity of pigeons for remembering an immense number of static images of natural scenes (Vaughan & Greene, 1984; see also Jitsumori & Ohkubo, 1996), it is not too surprising that the pigeons readily recognized a wide variety of static motion scenes as versions of the original moving scene.

GENERAL DISCUSSION

This series of experiments investigated perceptual and cognitive processes of pigeons in discriminating moving video images of other pigeons, focusing on effects of individuals, static and dynamic motion cues, and movement. Experiment 1 revealed that pigeons could discriminate the moving scenes on the basis of individuals (the bird discrimination group) or motion (the response discrimination group), depending on task requirement. The discrimination in both groups successfully transferred to novel scenes and even to the corresponding static scenes in Experiment 2. These findings led us to examine the extent to which motions (Experiment 3) and movement itself (Experiment 4) were used to recognize video scenes by pigeons. It was found that the motion cue that is invariant across static and dynamic conditions predominantly controlled pigeons' discrimination of video images, and that movement of different kinds (ecologically valid or not valid) was not salient for pigeons to discriminate dynamic scenes.

Individual Recognition

The findings in the bird discrimination group in Experiment 1 clearly indicated that pigeons can recognize

moving images of particular individuals regardless of their motions. The dominance of motion cues revealed in Experiment 3 suggests that training by using images of 2 different object birds in the same motion in Experiment 1 might have effectively prompted the pigeons in this group to discriminate the stimuli on the basis of the object cue that would otherwise be overshadowed by the motion cue. Thus pigeons seem to be able to abstract some visual information that enables them to recognize individuals. This information is perceptually invariant with respect to the movements shown by those individuals, since it was revealed in Experiment 2 that the discrimination readily transferred to the static scenes.

In contrast to the difficulties reported by Ryan and Lea (1994) in teaching pigeons to discriminate static images of individuals, the rapid acquisition shown by the pigeons in the bird discrimination group suggested that movement is critical for pigeons to learn discrimination of particular birds. When a static object (a stuffed pigeon) is presented at different depth orientations, or its two-dimensional representations (slides of a pigeon) are presented during the acquisition phase, perceptual features change discontinuously from trial to trial. Some parts are occluded and others come into view. Thus, the discrimination task requires subjects to infer unperceived rotations of an object bird across trials. Rotation-invariant recognition has been studied in pigeons by Cerella (1977, 1990a, 1990b), Lumsden (1977), and more recently by Wasserman et al. (1996). Wasserman et al. obtained clear evidence that pigeons reliably generalized discrimination of line drawings (an airplane, a chair, a desk lamp, and a flashlight) over untrained depth orientations. The types of objects depicted in their experiments are discriminably different from one another, whereas pigeons are very similar in general appearance and inherently difficult to be discriminated as individuals, at least for human observers. Although we do not know what pigeons see in two-dimensional photographs or in videos, it is likely that they would have difficulty in recognizing still images of their conspecifics presented in different orientations, a notion consistent with the findings of Ryan and Lea (1994). In contrast, moving stimuli yield images of an object continuously changing its orientation in depth within a trial. This might have enabled the pigeons in the bird discrimination group to learn to discriminate the moving scenes on the basis of the individuals that were shown. Specifically, the scene of circling used for training allowed the pigeons to see the object birds from virtually all directions. Movement may be critical for pigeons to learn individual recognition in the sense that distinctively different views and their structural relations could be integrated as a unified object. The finding that the pigeons in the bird discrimination group treated a variety of static scenes as versions of the original moving scene indicated that the pigeons had learned the rotation-invariant recognition of static images of individuals. However, all the static scenes tested in the present study were frozen frames selected

from the moving scenes used for training. It would be interesting in future research to examine how pigeons react to novel static scenes, or hidden views, of individuals. Given the present finding that pigeons can recognize moving images of individuals regardless of their motions, we speculate that they would successfully discriminate novel static scenes.

Motion Cue and Movement

An unexpected finding is that even the pigeons in the response discrimination group readily transferred their discrimination to the still scenes in Experiment 2. This finding was confirmed in Test 2 of Experiment 4 by using video scenes of pigeons showing a variety of activities in a natural setting. This led us to conclude that, although motion is highly salient for pigeons, as revealed in Experiment 3, movement itself is not critical for pigeons to recognize known video scenes. It is likely that information of motion scenes that was common to both the moving and the corresponding static scenes might have produced this result. This is not to say that movement is not necessary for pigeons to identify individual conspecifics and their motions. We suggest instead that pigeons are able to abstract information, or features, that is invariant with respect to the viewing conditions (static and dynamic). We may evaluate this notion in light of the findings of Dittrich and Lea (1993). They demonstrated, by using a modified discriminative autoshaping procedure, that pigeons can discriminate moving video scenes from the corresponding still scenes. This was found in the group of pigeons to which food was given only in association with moving images. The other group of pigeons, to which food was given only after still images, showed no evidence of discrimination during acquisition training. That is, pigeons' responding was not selectively inhibited in the presence of the negative moving stimuli. Dittrich and Lea interpreted their findings as a feature-positive effect, but the question of why moving stimuli elicited but failed to inhibit pigeons' behavior was left open. The findings of the present study indicate that information regarding particular scenes, regardless of whether static or dynamic, is salient for pigeons to discriminate video images. The failure to inhibit responding to the negative moving stimuli shown by the pigeons of Dittrich and Lea is now well explained by assuming that scene information that was common to the moving and the corresponding still scenes overshadowed the effect of movement in the negative stimuli—an explanation similar to the feature-negative effect proposed by Jenkins and Sainsbury (1970).

Perception of Two-Dimensional Video Images

We do not really experience a video image presented on a 2-D (two dimensional) display as being "truly" 3-D. Nevertheless, we can "see" real objects in 2-D photographs and in videos. Patterson-Kane et al. (1997) argued that animals, including humans, may learn to "see" real objects because there are consequences for learning, often

provided by interactions with the objects (Gibson, 1986). Although our pigeons clearly showed invariance with respect to the viewing conditions, it may be too early to tell whether pigeons recognize static scenes as depicting a particular bird that changes its images as it moves through 3-D space and time. Rather, the finding in Experiment 4 that the play direction of the video display did not affect discriminative performance of the pigeons raises the question of whether video animation is in fact perceived as smooth motion by pigeons. Pigeons have a higher flicker-fusion threshold than humans (Emmerton, 1983; Hendricks, 1966; Powell, 1967). The video monitor (60 Hz), designed for the human eye (for which the frequency is about 50 Hz at the approximate brightness of the video monitor), possibly breaks up the image for pigeons. In addition, the video player used in the present study displays 30 frames per second, and it is possible that pigeons have some kind of stroboscopic view. Is it possible that the stroboscopic effects of moving video sequences, if any, promoted the pigeons' transfer to the static scenes? To answer this, further study on pigeons' perception of moving video images would be required, which might also provide us with reliable techniques for exploring motion processing of birds, including pigeons.

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