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The Discrimination of Natural Movement by Budgerigars (*Melopsittacus undulates*) and Pigeons (*Columba livia*)

Rosetta Mui, Mark Haselgrove, Anthony McGregor,
and James Futter
Cardiff University

Cecilia Heyes
University College London

John M. Pearce
Cardiff University

Three experiments examined the ability of birds to discriminate between the actions of walking forwards and backwards as demonstrated by video clips of a human walking a dog. Experiment 1 revealed that budgerigars (*Melopsittacus undulates*) could discriminate between these actions when the demonstrators moved consistently from left to right. Test trials then revealed that the discrimination transferred, without additional training, to clips of the demonstrators moving from right to left. Experiment 2 replicated the findings from Experiment 1 except that the demonstrators walked as if on a treadmill in the center of the display screen. The results from the first 2 experiments were replicated with pigeons in Experiment 3. The results cannot be explained if it is assumed that animals rely on static cues, such as those derived from individual postures, in order to discriminate between the actions of another animal. Instead, this type of discrimination appears to be controlled by dynamic cues derived from changes in the posture of the demonstrators.

Keywords: movement discrimination, budgerigars, pigeons, dynamic cues

The behavior of one animal is often affected by the behavior of another animal, as the following examples illustrate. Burmese jungle fowl are more likely to peck at a distinctive dish if they have observed conspecifics engage in the same activity (McQuoid & Galef, 1992, 1993); budgerigars that observe another budgerigar remove a stopper from a box to obtain food tend to copy this action (Mottley & Heyes, 2003); and the courtship behavior of a bird such as the western grebe can be intricately related to the behavior of its partner (Nuechterlein & Storer, 1982).

The obvious implication of these diverse examples is that animals are able to tell the difference between the various actions and movements of other animals and to react accordingly. Given this conclusion, the question then arises as to how such discriminations are made. When any animal engages in a natural movement it can be regarded as executing a sequence of postures. It is possible that an animal discriminates between the actions of another animal on the basis of the information provided by a single posture from this sequence. For example, the sight of a bird bent over with its beak touching a container might have been sufficient to make the observers in the study by McQuoid and Galef (1993) perform the same response. In the study by Mottley and Heyes (2003), the observers may have simply copied the relevant postures of the demonstrators, rather than entire movements. And a stance offered during a courtship display may be sufficient to encourage the partner to react in a certain manner.

A particular posture can be described as a *static cue*, because it does not depend upon the movement of the demonstrator for it to occur. All that is necessary is for the observer to detect a single posture within an activity and to use this posture to identify the activity. Of course, sufficient information for the discrimination to be successful could be derived from either the single posture as a whole, or from a relevant fraction of it. It is not of present concern to choose between these alternatives, and we thus regard static cues as emanating from individual postures of the demonstrator without considering their nature in more detail.

Rather than refer to static cues, the actions of a demonstrator might be identified by the movement that is created. Any activity will generate what we refer to as *dynamic cues*, which depend upon changes in posture for their existence. Thus it might have been the sight of a demonstrator's beak moving toward and away from the bowl that had an effect on the behavior of the observers in the studies by McQuoid and Galef (1992, 1993), or the sight of the demonstrator actually moving the stopper in the study by Mottley and Heyes (2003) that encouraged the observers to engage in this activity, or the sight of an elaborate sequence of postures in a courtship display that resulted in a response by the partner (Nuechterlein & Storer, 1982). A major concern of the present article is to determine whether animals make use of such dynamic cues when discriminating between the actions of other animals.

Rosetta Mui, Mark Haselgrove, Anthony McGregor, James Futter, and John M. Pearce, School of Psychology, Cardiff University, Cardiff, Wales, United Kingdom; Cecilia Heyes, Department of Psychology, University College London, London, England.

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Correspondence concerning this article should be addressed to John M. Pearce, School of Psychology, Cardiff University, Tower Building, Park Place, PO Box 901, Cardiff, Wales, United Kingdom CF10 3YG. E-mail: pearcejm@cardiff.ac.uk

The first demonstration in the laboratory that one animal can solve a discrimination based on the movements of another animal was reported by Dittrich, Lea, Barrett, and Gurr (1998). They found that a pigeon could master a discrimination between video clips showing another pigeon either pecking or walking (see also Lea & Dittrich, 2000, for a similar finding with bantam hens using the same stimuli). Because the postures of a demonstrator who is pecking will differ from those of a demonstrator who is walking, it is impossible to know whether the discrimination was based on static or dynamic cues. Results described by Jitsumori, Natori, and Okuyama (1999) lend support to the first of these possibilities. The design of one of the reported experiments was similar to that used by Dittrich et al., except that the video clips were of demonstrators engaged in either key pecking or turning in circles. Once the discrimination between these activities had been acquired, test trials revealed that it was maintained when subjects were shown individual frames of different postures from the two clips. This outcome would be expected if the discrimination between the two activities were based on static cues. In a further experiment, Jitsumori et al. showed subjects two video clips of a pigeon engaged in different activities. Subsequent test trials in which the clips were played in the opposite direction to that used for training had no impact on the discrimination. If birds solved the discrimination by referring to the sequence of movements within a clip, then it might be thought that reversing this sequence would impair the discrimination. Instead, the results again implied that the birds solved the discrimination by learning about the significance of particular postures from the clips. In support of this conclusion, additional test trials revealed that birds were able to discriminate accurately between still frames from each of the two video clips.

Many studies of the perception of human movement have involved point-light displays (e.g., Johansson, 1973, 1975). Blake (1993) used similar stimuli in a study with cats, who were given a discrimination between a point-light animation of a cat walking forwards on a treadmill and the same animation but with the points rearranged so that they no longer corresponded to the shape of a cat. The cats acquired the discrimination, which transferred to a test with a sequence based on a cat running and, after a small amount of training, to an animation based on a human walking. Blake concluded from these results that cats can perceive biological motion created by moving points of light. Given the nature of the stimuli that were used, it is not possible to determine from Blake's results whether cats can go one step further and discriminate between different types of biological motion using point-light stimuli. In an attempt to address this issue, Dittrich et al. (1998) gave pigeons a discrimination using point-light stimuli that depicted pigeons walking or pecking. Four out of the eight birds acquired the discrimination, which suggests that at least some animals are capable of discriminating different types of biological motion depicted by point-light displays. This finding is difficult to interpret because it is likely that the two natural movements created different configurations of points of light. The discrimination could thus have been based on either static cues created by the different configurations, or by dynamic cues derived from the movement of the points of light (Beintema & Lappe, 2002).

In another experiment, Dittrich et al. (1998) trained pigeons to discriminate between demonstrator birds that were either walking or stepping. The birds were then shown point-light versions of the demonstrators, and they demonstrated a small but significant discrimination between the two movements. Although Dittrich et al. concluded that this successful transfer demonstrates that the birds used dynamic cues to solve the discrimination, it is noteworthy that subjects were rewarded for responding during the correct but not the incorrect point-light display. It is thus possible that the successful discrimination during testing was due to new learning based on static cues provided by the point-light images rather than on any control by dynamic cues acquired during the initial training.

There is, therefore, rather little evidence that animals refer to dynamic cues when discriminating between different natural movements of other animals. In order to determine if the discrimination of natural movement can be based on dynamic cues, the following experiments adopted a rather different design to the studies just described. Subjects were shown a video clip of demonstrators walking forwards, and they were also shown the same video clip but modified so that it showed the demonstrators walking backwards. The actions depicted in the two video clips were therefore composed of the same frames and hence depicted the same array of postures. However, the sequence in which these postures were presented varied between the video clips. Thus the discrimination could not be solved by referring to static cues based on individual postures. Instead, its solution might be based on dynamic cues created by the transitions from one posture to another, or from one frame to another. Although this rationale lay behind each of the reported experiments, it shortly became evident that alternative explanations for the successful solution of this discrimination were possible and that additional tests were needed to eliminate them.

Experiment 1

For the first experiment, a group of budgerigars was shown on a computer monitor a video clip of demonstrators walking forwards and a modified version of the same clip showing the demonstrators walking backwards. Given the shortcomings of using cathode ray tube displays for presenting moving images to animals (D'Eath, 1998; Mottley & Heyes, 2003), we used thin film transistor (TFT) liquid crystal displays. The experimental subjects were budgerigars because they can discriminate between different actions shown on TFT displays (Mottley & Heyes, 2003). We had intended to use a budgerigar as the demonstrator for walking, but our attempts to record one walking in a straight line were thwarted by the bird's reluctance to engage in this activity for more than a few steps before changing to some other activity. Accordingly, it was decided to use a female human and a dog walking on a leash as the demonstrators. The combination of the human and dog was intended to provide a richer source of movement cues than a human alone.

Initially, the budgerigars were shown a video clip of the person and dog walking either forwards or backwards from left to right across the screen. Examples of single frames from each of the clips can be seen in the left half of Figure 1. Responding in the presence of one of these clips (S+) resulted in the delivery of food, whereas responding in the presence of the other clip (S–) never resulted in food. The assignment of the clips to S+ and S– was counterbalanced across subjects, and Figure 1 shows this assignment for the birds who were reinforced for responding during the clip of the demonstrators walking forwards.

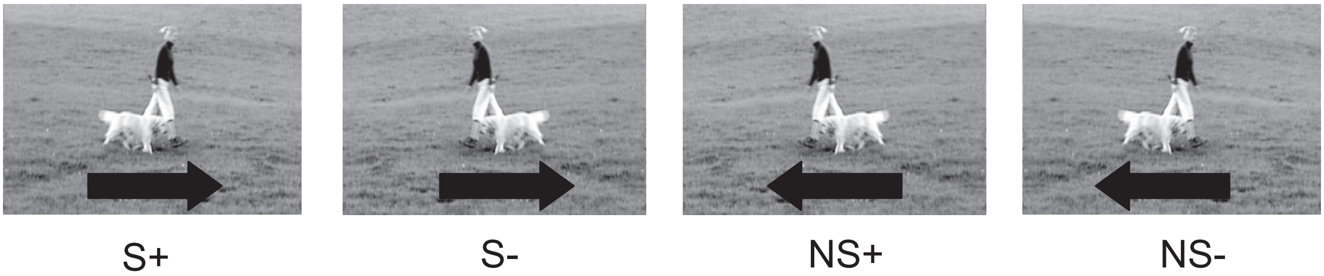

Figure 1. Frames selected from the four video clips that were shown in Experiment 1 and Stages 1 and 2 of Experiment 3. The same images, but with larger demonstrators, were used in Experiment 2 and in Stages 3 and 4 of Experiment 3. The arrows depict the direction in which the demonstrators were heading.

The solution of the discrimination between the two clips shown in the left half of Figure 1 would be of little theoretical interest because it could be solved on the basis of a static cue, for example, whether the person and dog were facing to the left or right. Even so, we used these video clips at the outset of the experiment in order to confirm that the birds could discriminate between our training stimuli. After the completion of this training, we conducted a test session to identify the cues on which the original discrimination was based. Four different video clips were shown in the test session. Two of the clips were those shown during the initial training. The two new clips (NS+ and NS–) were of the person and dog walking either forwards or backwards and moving across the screen from right to left, which was opposite of that shown in S+ and S–. Examples of frames from these clips can be seen in the right half of Figure 1. One frame is labeled NS+ because it was taken from the new clip of the demonstrators walking in the same direction (forwards) as shown in S+. The other frame is labeled NS– because the demonstrators are walking in the same direction (backwards) as shown in S–. If the original discrimination were based on whether the demonstrators were facing to the left or right, then responding during NS+ should be at a similar rate to that during S–, and responding during NS– should be similar to that during S+.

Another possibility is that during their original training the budgerigars discriminated between the two clips by using a dynamic cue consisting of the actions performed by the demonstrators—if they were walking forwards or backwards. On this basis, responding during NS+ should be similar to that recorded during S+, and responding during NS– should be similar to that during S–.

Method

Subjects. The subjects were 9 adult budgerigars (*Melopsittacus undulates*) of both sexes and of unknown age, but who were at least 9 months old at the start of the experiment. Their weights ranged from 33 to 50 g. They were housed together in a cage (88 × 40 × 30 cm; height × width × depth) in a holding room with a 12:12-hr light–dark cycle and a temperature of 19 ± 2º C. The birds had free access to water, cuttlebone, grit, and water baths. During the experiment they were weighed daily and maintained at 85% of their free-feeding weights by being fed a restricted amount of food after each experimental session. The food was Budgie Mix (H. G. Gladwell & Sons, Ipswich, United Kingdom), which is a mixture of canary seed and white and red millet. On days when the experiment was not performed, subjects were given a free supply of food that was removed 16 hr before testing resumed. Prior to the start of the experiment, all subjects received discrimination training for which the stimuli consisted of video clips either of an empty chamber or of a budgerigar standing in the chamber.

Apparatus. Four conditioning chambers (25 × 25 × 25 cm) constructed from clear Perspex were housed in separate light- and sound-attenuating chests (78 × 46 × 44 cm). A color TFT monitor (ViewSonic, VS10057) with a screen that was 27 cm high and 34 cm wide was attached to the left-hand side wall of each chest. The midpoint of the screen was 20 cm above the floor, 20 cm from the rear wall, and 8.5 cm from the left-hand side wall of the chest. The wall of each conditioning chamber that was nearest to the TFT screen was hinged at the bottom to serve as a door. This door was parallel to the TFT screen and 40 cm from it. The floor of each chamber was 6 cm above the floor of the chest. During the experiment Budgie Mix was made available by a grain dispenser (Colbourn Instruments, Lehigh Valley, PA) that was attached to the wall to the left of the door of the conditioning chamber. The grain feeder had an opening that was 5 × 6 cm. The midpoint of the opening was 3.5 cm above the floor of the chamber and 7 cm from the door. A square Perspex response box with sides of 6 cm and with a lid on top was located on the floor of the conditioning chamber. The top of the lid was 0.5 cm above the floor of the chamber, and its midpoint was 4 cm from the door and 12 cm from the wall containing the grain feeder. The sides of the response box were red, and the lid was blue. A microswitch operated whenever a force of greater than 6 gm was applied to the lid. A closure of this switch for more than 10 ms was recorded as a response. The floor of each conditioning chamber, except for the response box, was covered with cage-lining paper. Illumination in the conditioning chambers was provided by the events on the TFT screen and by a bulb in the grain feeder that was turned on whenever grain was made available. The presentation of stimuli on the TFT screens, the recording of responses, and the operation of the grain feeder were controlled by a PC computer (Research Machines, Abingdon, United Kingdom) running Windows XP. The computer was programmed in VisualBasic, and the interface with the experimental apparatus was controlled by Whisker software (Campden Instruments, Loughborough, United Kingdom).

Video stimuli. The video clips shown in the experiment were all based on a recording made in color by a digital video camera (Sony Handycam DCR-HC30E) of an adult female person leading a golden retriever dog at the end of a 1-m leash. The camera was stationary during recording so that the video clip consisted of the demonstrators walking from left to right against a static background that was grass on the bank of a steep hill. When this clip was played on the TFT screen, an interval of 4 s elapsed between the time that the demonstrators appeared on one side of the screen and disappeared from the other side. The height of the person on the screen was 9 cm, and her feet were 13 cm above the bottom of the screen.

The original clip was edited using Adobe Premiere Pro 1.5 to create four clips: the original clip of the demonstrators walking forwards from left to right, a horizontal flip of the original to show the demonstrators walking forwards from right to left, a reverse of the original to show the demonstrators walking backwards from right to left, and a reverse of the original clip that was flipped horizontally to show the demonstrators walking backwards from left to right. Each clip was repeated 30 times to create a looped display that lasted for 120 s.

Procedure. All of the subjects had been hand shaped in a previous experiment to step on the response box in the conditioning chamber in order to operate the grain feeder. Because of this training, and the subsequent discrimination training that was given in the earlier experiment, no additional training was given before the start of the present experiment.

The experiment was conducted over 47 sessions that took place at the same time each day, 5 days a week. During each of the first 46 sessions, the clips of the demonstrators walking either forwards or backwards from left to right across the screen were each presented seven times, for 2 min at a time, in a random sequence with the constraint that the same clip was not shown more than twice in succession. There was an interval of 20 s before the first video clip was shown, and there was an interval of 10 s between successive clips. The TFT screens were entirely white during these intervals. Food was made available for stepping on the box according to a variable-interval (VI) 30-s schedule during the clip of the demonstrators walking forwards for 4 budgerigars, and during the clip of the demonstrators walking backwards for the remaining 5 budgerigars. A new value for the VI schedule was selected at the start of every trial. The same VI schedule was in operation during the trials with the other video clip, but food was never presented on these trials. The number of responses made during the first interval selected from the VI schedule was recorded on every trial. These numbers were then used to calculate individual mean rates of responding for all of the reinforced and all of the nonreinforced trials of every session. Note that because these response rates were obtained before food was delivered, they reflect solely the influence of the video clips on responding.

The training that has just been described was continued for a final, test session of the experiment, but in this test session there were four extra trials with clips for the first time of the demonstrators walking from right to left across the screen. For two of these trials the demonstrators were walking forwards, and for the other two they were walking backwards. The trials were presented at randomly selected points among the original training trials in an alternating sequence. Food was not presented during the trials with the two new video clips.

Results

A Type I error rate of $p < .05$ was adopted for all statistical tests.

The left-hand panel of Figure 2 shows the group mean rates of responding, in two-session blocks, during presentations of the video clip that signaled food was available (S+) and during the clip that signaled food was not available (S–). The rate of responding was soon faster during S+ than S– trials. A two-way analysis of variance (ANOVA) of individual mean response rates for each two-session block revealed a significant effect of stimulus, *F*(1,

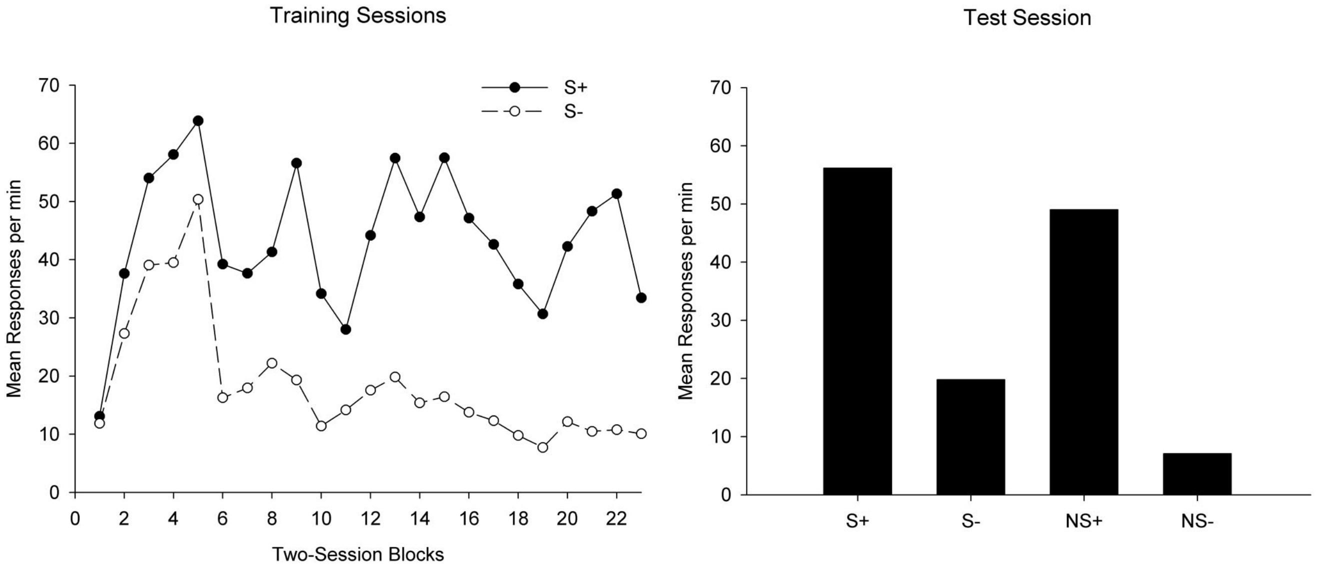

Figure 2. The mean rates of responding during the video clips that served as S+ and S– for the training sessions of Experiment 1 (left-hand panel), and the mean rates of responding in the test session during the trials with the same video clips and with two new clips, NS+ and NS– (right-hand panel).

8) = 9.04; of two-session block, $F(22, 176) = 2.62$; and a significant interaction, $F(22, 176) = 2.68$. Subsequent tests of simple main effects revealed that responding was significantly faster during S+ than S– trials for Session Blocks 9 and 10 and from Session Block 12 onward, $Fs(1, 184) > 4.77$.

The results from the final test session can be seen in the right-hand panel of Figure 2, which shows the group mean rates of responding during the seven trials with each of the original video clips (S+ and S–) and the two trials with each of the test video clips (NS+ and NS–). Recall that the demonstrators were walking in the same direction (either forwards or backwards) in S+ and NS+ and in the opposite direction in S– and NS–. The rate of responding during S+ and S– was much the same as that during the final sessions of discrimination training. Likewise, responding was rapid during NS+ and slow during NS–, but it appeared that responding was slower during the test clips than the training clips. A two-way ANOVA of individual mean rates of responding during each of the four different types of trial revealed a significant effect of direction of walking (forwards or backwards), $F(1, 7) = 8.0$, and a significant effect of video clip (training or new), $F(1, 7) = 6.31$. The interaction between these factors was not significant, $F < 1$.

A clear conclusion to be drawn from these results is that the discrimination between the training patterns was not solved on the basis of the direction in which the demonstrators were facing. During the two video clips shown throughout the training stage, the demonstrators were facing in one direction during S+ trials and in the opposite direction during S– trials. If subjects had relied on this difference between the clips to solve the discrimination, then they should have responded rapidly during the NS– video clip in which the demonstrators were facing in the same direction as during the S+ trials. Responding was slow on these test trials. Conversely, they should have responded slowly during the NS+ video clip in which the demonstrators were facing in the same direction as for the S– trials. Responding was fast on these test trials.

Although the results are consistent with the claim that the discrimination between S+ and S– was based on the dynamic cue of whether the demonstrators were walking forwards or backwards, an alternative, static-cue explanation can be developed for the findings of the experiment. During their initial training, subjects may have paid no attention to the sequence of postures exhibited by the demonstrators; rather, they may have focused on the relationship between the direction in which the demonstrators faced and the direction in which they moved. When walking forwards, the demonstrators would be moving in the direction they are facing, whereas when walking backwards they would be moving away from the direction they are facing. If subjects detected this relationship, then not only would they solve the original discrimination, but they would also respond correctly during the test video clips. Experiment 2 was conducted in order to test this account for the results that have just been described.

Experiment 2

The birds that were used in Experiment 1 were also used in Experiment 2, and they were shown video clips based on those depicted in Figure 1. The principal difference between the experiments is that instead of walking across the screen, the demonstrators were shown walking in place, as if they were on a treadmill, in the middle of the screen. For the first stage of the experiment, the demonstrators were walking forwards facing to the right, and walking backwards facing to the left (see two left-hand panels of Figure 1). If subjects had solved the discrimination in Experiment 1 by focusing on the relationship between the directions in which the demonstrators were facing and moving, then once the demonstrators were stationary it should no longer be possible to solve the discrimination. As for the previous experiment, the successful solution of this discrimination would not necessarily imply that subjects were discriminating between the two video clips on the basis of the dynamic cues relating to the movements of the demonstrators. The direction they were facing by itself would provide a sufficient static cue for distinguishing between the two video clips. However, we decided to train the birds initially with these two clips in order to provide them with a relatively simple problem before they were exposed to test trials designed to identify the cues that were used to solve the discrimination.

After 30 sessions of the training that has just been described, the group showed no indication of having solved the discrimination. One possible explanation for this failure is that the demonstrators occupied a relatively small region of the screen and it may have been difficult for the birds to perceive the movements they made. Accordingly, the video clips were modified by increasing the size of the demonstrators. This change was followed by the development of a successful discrimination between the two video clips during a subsequent 20 sessions of training.

Upon the completion of the training, the group received a single test session that was conducted in much the same way as the test session of Experiment 1, except that the demonstrators remained stationary in the middle of the TFT screen. There were four video clips shown in the test session: two that were used for the initial training (S+ and S–) and two new ones (NS+ and NS–). The new clips were of the demonstrators either walking forwards facing to the left or walking backwards facing to the right (see Figure 1). If the original discrimination was based on the dynamic cues of walking forwards or backwards, then during the test trials with the new patterns, the strength of responding would be determined by the direction of walking. In contrast, if the original discrimination was based on the direction that the demonstrators were facing, then this factor should determine responding during the two new video clips.

Method

Subjects, apparatus, and video stimuli. The subjects and apparatus were the same as for Experiment 1. The original video clip that was used for Experiment 1 was edited to create a video clip of the person and dog walking, without moving, in the center of the TFT screen. To prepare this clip, the torso of the woman was used as the central point of each frame, and the remaining objects were moved relative to this reference point. The edited clip was modified further to create three additional clips: the demonstrators walking backwards facing to the left, the demonstrators walking backwards facing to the right, and the demonstrators walking forwards facing to the right. The height of the person on the screen was originally 9 cm, but this was increased to 22 cm. Each video clip lasted for 2 min.

Procedure. Experiment 2 commenced 19 days after the completion of Experiment 1. For each of the first 50 sessions of the experiment, there were seven trials with the video clip of the demonstrators walking forwards and facing to the right, and seven trials with the demonstrators walking backwards facing to the left. The height of the person in the video clips was 9 cm for the first 30 sessions and 22 cm for the remainder of the experiment. Stepping on the response box was rewarded with access to grain according to a VI 30-s schedule during the video clip of the demonstrators walking forward for the 4 budgerigars for whom S+ in the previous experiment had also been of the demonstrators walking forwards. The video clip of the demonstrators walking backwards served as S–. This relationship between the video clips and the availability of food was reversed for the remaining birds. In Session 51 there were seven trials with each of S+ and S–, plus two trials with each of the remaining two video clips, NS+ and NS–. Procedural details that have been omitted were the same as for the previous experiment.

Results

The mean rates of responding during the two types of trial for the 50 sessions of discrimination training, in two-session blocks, are shown in Figure 3. The group failed to discriminate between S+ and S– during the first 30 sessions, but when the image of the demonstrators was increased in size for the remaining 20 sessions, then a faster rate of responding during S+ than S– became evident. A two-way ANOVA of individual mean response rates for the final 10 two-session blocks revealed a significant effect of session block, $F(9, 63) = 3.25$, and a significant Session Block × Stimulus interaction, $F(6, 63) = 2.85$. Subsequent tests of simple main effects revealed that responding was significantly faster during S+ than S– for the final 4 two-session blocks, $Fs(9, 63) > 5.00$.

The histograms in the right-hand panel of Figure 4 show the results from the test session. In keeping with the results from the final session of training, responding was more vigorous during S+ than S–. In addition, responding during the new clips was faster during NS+, for which the direction of walking (forwards or backwards) was the same as during S+, than during NS–, for which the direction of walking was the same as during S–. A two-way ANOVA of individual mean response rates during the four video clips shown in the test session revealed a significant effect of the direction of walking, $F(1, 7) = 14.14$, but the effect of whether the clips were original (having been shown throughout training) or novel (introduced for the test session) was not significant, $F < 1$, and the interaction was not significant, $F < 1$.

The successful discrimination between the two video clips used for the training trials could have been based on a dynamic cue (i.e., whether the demonstrators were walking forwards or backwards). Alternatively, the discrimination could have been based on a static cue (i.e., the direction that the demonstrators were facing). The results from the two new video clips introduced in the final test session revealed support for the first of these interpretations but not the second. Moreover, because the same video footage was used to create the four video clips, it was not possible to discriminate between them in terms of the postures shown by individual frames. The experiment thus provides a clear demonstration that one species of bird, the budgerigar, is able to discriminate between two different natural movements using information provided by the transitions from one posture to another during the course of these movements.

Experiment 3

The principal purpose of the final experiment was to confirm the reliability and generality of the foregoing results by determining

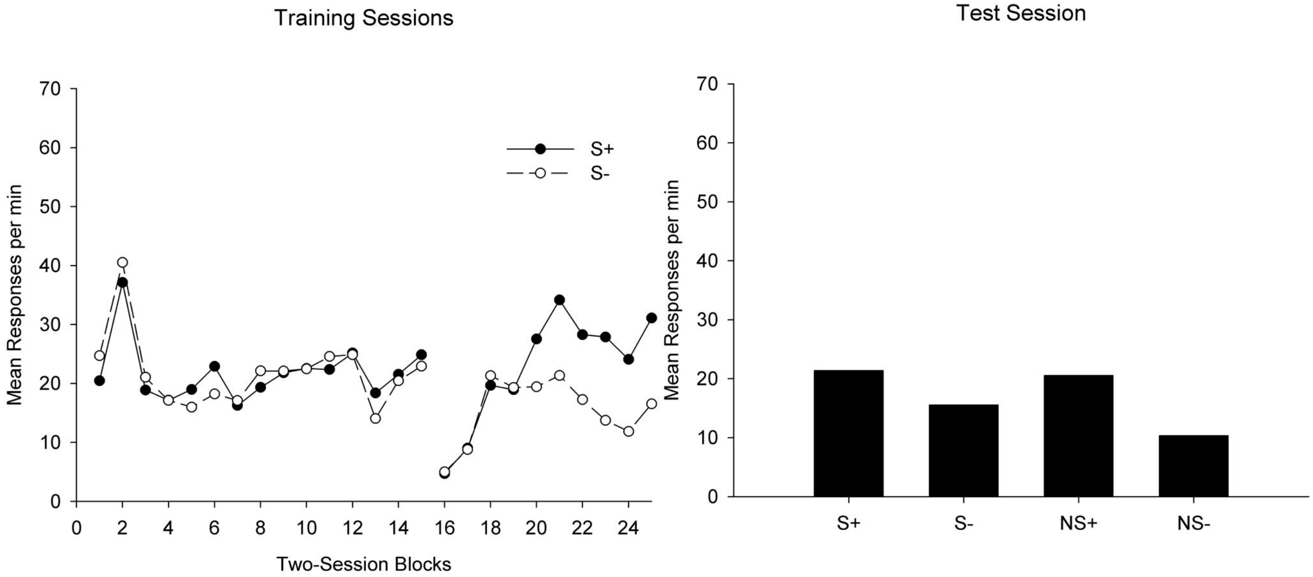

Figure 3. The mean rates of responding during the video clips that served as S+ and S– for the training sessions of Experiment 2 (left-hand panel), and the mean rates of responding in the test session during the trials with the same video clips and with two new clips, NS+ and NS– (right-hand panel).

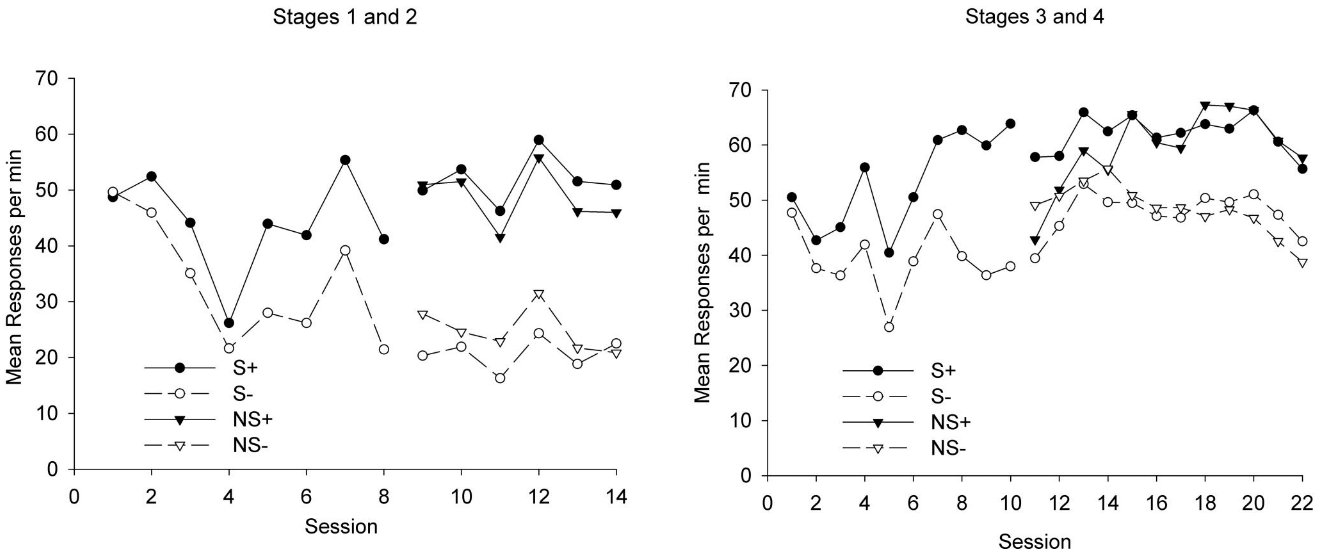

Figure 4. The mean rates of responding for Experiment 4 during S+ and S– in Stage 1; during S+, NS+, S–, and NS– in Stage 2 (left-hand panel); during S+ and S– in Stage 3; and during S+, NS+, S–, and NS– in Stage 4 (right-hand panel). The training stimuli during the first two stages were video clips of demonstrators walking across a thin film transistor screen, whereas for the last two stages, the stimuli were video clips of demonstrators walking as if on a treadmill.

whether they could be obtained with a more conventional laboratory subject, the pigeon. A single group of pigeons received four stages of training with a number of sessions in each stage. During Stage 1, the birds were given the same discrimination that had been used for the training stage of Experiment 1 (see the left-hand half of Figure 1). That is, they were required to discriminate between video clips of the demonstrators walking, either forwards or backwards, from left to right across the screen. The group was then shown, for Stage 2, the four clips that had been used for the test session of Experiment 1 (see all of Figure 1). However, rather than repeat the test session of Experiment 1, the four clips were used for a new discrimination in which the two clips of the demonstrators walking forwards signaled one outcome, and the two clips of the demonstrators walking backwards signaled the other outcome. After the completion of Stage 2, the birds progressed to Stage 3, in which the two video clips of the demonstrators walking as if on a treadmill that had been used for the training stage of Experiment 2 were used for discrimination training. For the final stage of the experiment, the four clips shown in the test session of Experiment 2 were used for a number of sessions of discrimination training. Throughout the experiment, responding was reinforced according to whether the demonstrators were walking forwards or backwards.

The results from the test trials of Experiment 1 and, particularly, Experiment 2 have been regarded as being of some theoretical importance. However, the critical results from the tests were obtained from only two presentations of the video clips that were introduced in the test sessions. There was a concern, therefore, that the discrimination between these new clips might not be particularly robust. It was in order to explore this possibility that instead of including test sessions in Experiment 3, we used the four clips for a number of sessions of discrimination training. If the capacity to tell the difference between walking forwards and backwards is robust, then the discrimination between the video clips introduced in Stages 2 and 4 will be acquired rapidly and sustained with little difficulty.

Method

Subjects. Sixteen adult experimentally naïve pigeons (*Columba livia*) of both sexes were used for the experiment. They were housed in pairs in a vivarium that had a 12-hr light–dark cycle and that was maintained at 19 ± 2° C. There was free access to water and to grit in the home cages throughout the experiment. The birds were maintained at 80% of their free-feeding weights by being fed a restricted amount of food after each experimental session. Prior to the present experiment, all birds were given a red–green discrimination with stimuli shown on a TFT screen.

Apparatus. The apparatus was based on that used for Experiments 1 and 2 but it was larger and contained a different manipulandum. The dimensions of the soundproof chamber were 78 cm × 46 cm × 44 cm (width × depth × height). The dimensions of the clear Perspex conditioning chambers were 34 cm × 30.5 cm × 33 cm. The positioning of each conditioning chamber with respect to the TFT screen was similar to that in Experiment 1, but the distance between the wall of the chamber nearest to the screen and the screen was 35 cm. A Colbourn Instruments (Lehigh Valley, PA) grain feeder was attached to the wall of the conditioning chamber that was nearest to the door of the soundproof chamber. The center of the opening of the grain feeder was 12.5 cm above the floor of the conditioning chamber and 6.5 cm from the left-hand wall. The wall of the conditioning chamber that was nearest to the TFT screen was hinged at the bottom to serve as a door. The center of a Campden Instruments (Loughborough, United Kingdom) 1-cm circular pigeon response key was located 13.5 cm above the middle of the opening of the grain feeder. The key could be illuminated with white light. Pecks at the response key were detected by the closure of a reed relay. The remaining details of the apparatus were the same as for Experiment 1. The video clips for the experiment were the same as those used for Experiments 1 and 2.

Procedure. Two days after the completion of their training with a red–green discrimination, the birds received eight sessions of training in Stage 1 of the present experiment. In each session, 8 of the birds were shown the video clip of the demonstrators walking forwards from left to right across the screen as S+, and the video clip of the demonstrators walking backwards from left to right as S–. The opposite assignment of the video clips to S+ and S– was used for the remaining birds. The duration of each trial was 60 s. There was an interval of 10 s between each trial, during which the TFT screen was entirely white. No more than two trials of the same type occurred in succession, and there were 40 trials in a session (20 with S+ and 20 with S–). Pecking on the response key during S+ but not S– was reinforced according to a VI 30-s schedule.

Training continued in the manner just described with S+ and S– for the six sessions of Stage 2, but there were additional trials with the two video clips of the demonstrators walking from right to left across the screen. Food was made available for responding during the new clip NS+ if the demonstrators were walking in the same direction (either forwards or backwards) as for S+. Food was not made available during the other new clip (NS–) if the demonstrators were walking in the same direction as for S–. The four clips were each shown 10 times in each session. Other procedural details were the same as for Stage 1.

Stages 3 and 4 of the experiment were conducted in the same manner as Stages 1 and 2, respectively, except that instead of the demonstrators moving across the TFT screen, the video clips showed them in the middle, walking as if on a treadmill. There were 8 sessions in Stage 3, with two clips based on those used in Stage 1 that we again refer to as S+ and S–; and 13 sessions in Stage 4, with four clips based on those shown in Stage 2 that we refer to as S+, S–, NS+, and NS–. The height of the person on the screen was 22 cm throughout Stages 3 and 4. The remaining procedural details were the same as for Experiments 1 and 2. Throughout the experiment, the method for recording the rate of key pecking during each trial was the same as for Experiment 1. Thus, the response rates that are reported were obtained during a period commencing at the start of each trial, the duration of which was determined by the VI schedule.

Results

The results from the first two stages of the experiment are presented in the left-hand panel of Figure 4. The left half of the panel shows the group mean response rates during S+ and S– that were shown during Stage 1. The right half of the panel shows the equivalent results for the four video clips that were shown during Stage 2. The discrimination was acquired without much difficulty in Stage 1, and it was sustained throughout Stage 2. Moreover, the discrimination transferred immediately, and with only a moderate disruption, to NS+ and NS– when they were introduced at the start of Stage 2.

The foregoing observations were supported statistically. A two-way ANOVA of individual mean response rates for the eight sessions of Stage 1 revealed a significant effect of stimulus, $F(1, 15) = 21.72$; and of session, $F(7, 105) = 7.72$; and a significant interaction, $F(7, 105) = 8.42$. Subsequent tests of simple main effects revealed that responding was significantly faster during S+ than S– from Session 5 onward, $Fs(1, 120) > 23.06$.

The results from Stage 2 were analyzed with a three-way ANOVA with the factors of session, stimulus (reinforced or nonreinforced), and stage (whether the video clips had been shown in Stage 1 or were new to Stage 2). There was a significant effect of stimulus, $F(1, 15) = 27.95$; and of session, $F(5, 75) = 3.66$; and the Session × Stage, $F(5, 75) = 3.47$, and Stimulus × Stage, $F(1, 15) = 15.86$, interactions were also significant. Examination of the second of these interactions, using tests of simple main effects, revealed for all sessions combined that responding was significantly faster during S+ and NS+ combined than during S– and NS– combined, $Fs(1, 30) > 20.27$. In addition, responding was significantly faster during S+ than NS+, and significantly slower during S– than NS–, $Fs(1, 30) > 5.82$. To return to the overall analysis, the effect of stage was not significant, $F < 1$, nor were the two remaining interactions, $Fs < 1$.

The findings from the final two stages of the experiment can be seen in the right-hand panel of Figure 4. It is evident from the left side of this panel that the discrimination between S+ and S– from the previous stage was disrupted by showing the demonstrators walking as if on a treadmill, but the birds soon mastered this discrimination. It is further evident from the other side of the right-hand panel that introducing NS+ and NS– in Stage 4 weakened the discrimination between S+ and S– and resulted temporarily in a higher rate of responding during NS– than NS+. With continued training, the birds responded at a similar rate during S+ and NS+ that was faster than during S– and NS–.

A two-way ANOVA for the results from Stage 3 of the experiment revealed a significant effect of stimulus, $F(1, 15) = 17.83$; of session, $F(9, 135) = 3.95$; and a significant interaction, $F(9, 135) = 6.95$. Tests of simple main effects then revealed that responding was more rapid during S+ than S– from Session 3 onward, $Fs(1, 150) > 4.00$.

A three-way ANOVA for the results from Stage 4, which was similar to the analysis for Stage 2, revealed a significant effect of stimulus, $F(1, 15) = 14.63$. The Session × Stimulus, $F(12, 180) = 6.30$, and the Session × Stimulus × Stage, $F(12, 180) = 7.91$, interactions were also significant. Subsequent tests of simple main effects, to explore the three-way interaction, revealed that responding during S+ was significantly faster than during S– for every session of Stage 4, $Fs(1, 390) > 8.01$, and that responding was significantly faster during NS+ than NS– from the sixth session of this stage (Session 16 in Figure 4) onward, $Fs(1, 390) > 5.39$. In addition, responding during NS+ was slower than during NS– for the first session of Stage 4, $F(1, 390) = 8.74$. The remaining effects and interactions from the overall ANOVA were not significant: stimulus, $F(12, 180) = 1.48$; stage, $F(1, 15) = 1.47$; Session × Stimulus, $F(12, 180) = 1.10$; and Stimulus × Stage $F(1, 15) = 3.61$.

The results from the present experiment largely replicated the findings from Experiments 1 and 2. It thus appears that pigeons share with budgerigars an ability to discriminate between different natural movements. Having drawn this conclusion, we should acknowledge that the results revealed one difference between the performances of these species. Both pigeons and budgerigars were able to discriminate between the two video clips they were originally shown of the demonstrators walking forwards or backwards in place. Their performance when they were introduced to new video clips of these actions (NS+ and NS–) suggests, however, that they solved the original discrimination between the two clips of these actions in different ways. On first being exposed to the new clips, budgerigars in Experiment 2 immediately responded more rapidly to NS+ than NS–, which implies the original discrimination was based on the direction in which the demonstrators were walking. In contrast, when the pigeons were first exposed to these clips in Stage 4 they initially responded more rapidly to NS– than NS+. This result suggests that the pigeons solved the discrimination in Stage 3 by referring to the direction in which the demonstrators were facing, rather than whether they were walking forwards of backwards. The remaining results from Stage 4 demonstrate that pigeons were able to tell the difference between the directions in which the demonstrators were walking, but they appeared to be more reluctant than budgerigars to make use of this information. It is not clear on the basis of the available evidence how this difference between the two species can best be explained.

General Discussion

Two different types of cues can be used by an animal when it discriminates between the actions of another animal. We have referred to one type as a static cue because it can be derived from individual postures selected from the overall sequence of the behavior. The other type of cue has been referred to as dynamic because, to be perceived, it is necessary for the demonstrator to change from one posture to another. The present experiments were conducted in order to discover whether animals make use of dynamic cues when solving discriminations based on the natural movements of another animal. The most convincing evidence for the use of these cues was provided by the test trials of Experiment 2 and Stage 4 of Experiment 3. In the latter case, for example, pigeons were able to discriminate between stationary demonstrators walking forwards, facing either to the left or right, from the same demonstrators walking backwards, facing either to the left or right. The video clips of the demonstrators walking forwards were composed of the same frames as the clips of the demonstrators walking backwards, which means that by referring to individual postures from the two actions it would be impossible to solve the discrimination. Instead, it must have been solved on the basis of different dynamic cues arising from walking forwards and backwards.

Having established that animals are sensitive to dynamic cues, it then becomes important to identify these cues. According to Giese and Poggio (2003), two different types of dynamic cues provide information about biological movement, at least for mammals. One type is the optic flow emanating from the movement of images across the retina. Giese and Poggio argued that information about optic flow is processed by the dorsal stream. Neurons at the lower levels of this pathway are said to be sensitive to the local motion created by small components of the moving body. Neurons at higher levels are meant to be sensitive to the optic flow of the entire body as it changes from one posture to another. Ultimately in the dorsal stream there are predicted to be neurons that are sensitive to the optic flow created by an entire movement such as walking. Experiments have revealed that neurons in the pigeon brain may be sensitive to optic flow (e.g., Wang & Frost, 1992; Wylie, Bischof, & Frost, 1998). It may not, however, be easy to determine whether the optic flow created by the demonstrators in the present studies was responsible for the ability of our subjects to discriminate between them walking forwards and backwards. The problem is that the moving images shown to the birds were complex, which makes it extremely difficult to analyze the contribution made by optic flow to their performance.

The other type of dynamic cue is based on form and was said by Giese and Poggio (2003) to be processed by the ventral stream. At the lowest level of this pathway are neurons that are sensitive to lines at particular orientations. Higher up the pathway are neurons that are sensitive to snapshots of particular postures, and if these neurons are excited in a particular sequence then they will excite motion pattern neurons that will fire when one type of movement is observed. Thus, seeing a given sequence of snapshots might excite a motion pattern neuron for walking forwards, whereas observing the reverse of this sequence might excite a motion pattern neuron for walking backwards.

Perhaps, therefore, the subjects in our experiments discriminated between the two types of walking by taking note of the order in which the various postures were performed. A possible problem with this proposal is the finding that after subjects had been trained with the demonstrators walking forwards, say, from left to right, the discrimination transferred immediately to trials in which the demonstrators were walking forwards from right to left. This outcome was observed in the test trials of Experiments 1 and 2 and at the outset of Stage 2 of Experiment 3. If, as Giese and Poggio (2003) suggested, the postures in a currently observed action must correspond with snapshots of previous exemplars of this activity for the activity to be recognized, then it does not necessarily follow that recognition will be possible when the mirror image of the action is viewed. Indeed, Giese and Poggio suggested that recognition of movement, based on changes in posture, will be very difficult when the mirror image of an action is viewed for the first time. The implication of our results is that this type of recognition is less viewpoint dependent, at least for certain birds, than Giese and Poggio assumed.

Our results have implications not only for theories concerning the perception of natural movement, but also for theories of discrimination learning. George, Ward-Robinson, and Pearce (2001) argued that according to most of these theories (e.g., Pearce, 1987, 1994; Rescorla & Wagner, 1972), a discrimination between two patterns of stimulation will be possible only if the patterns are composed of different features. If two patterns consist of different arrangements of the same components, then, according to these theories, information about the structure of the patterns is ignored and the discrimination will be impossible to solve. If it is accepted that the discrimination of natural movement is based on an appreciation of the order in which a sequence of postures is executed, then the present results pose a similar problem for theories of discrimination learning because the theories do not explain how the order in which stimuli occur is encoded. As we have just seen, the theory of Giese and Poggio (2003) provides one solution to this problem by proposing that unidirectional associations develop between neurons that are successively activated as a sequence of postures from a given action is observed. Provided this sequence of neurons is activated in the correct order, a motion pattern neuron will be activated that will then effectively represent the action concerned. It remains to be determined, however, whether this type of associative mechanism is responsible for the discrimination of natural movement by animals.

Our results are of relevance to at least one theory of imitation in animals. The associative sequence learning model (Heyes, 2001, 2005) proposed that in order to imitate an action performed by another animal, it is necessary for the observer to form unidirectional, horizontal links between representations of successive postures made by the demonstrator. This type of analysis is clearly based on the assumption that animals are sensitive to the order in which an observed sequence of postures is performed, and it thus gains support from the present results.

The present experiments revealed that birds are able to discriminate between two movements that consist of the same postures performed in different sequences. We have argued that this discrimination is controlled by dynamic rather than static cues based on the sequence of postures executed by the demonstrators.

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