Budgerigars (*Melopsittacus undulatus*) Copy Virtual Demonstrators in a Two-Action Test

Kieron Mottley and Cecilia Heyes
University College London

Juvenile budgerigars (*Melopsittacus undulatus*) observed thin film transistor video playback of a virtual conspecific demonstrator using its beak to remove a stopper from a food box, either by pulling the object upward or by pushing it downward. Simultaneously (Experiment 1) or subsequently (Experiment 2), the observers were offered a similar stopper box and rewarded with access to food for each removal response, regardless of its direction. Observers of upward movement made a greater proportion of up responses in total and showed a stronger tendency to increase the proportion of up responses over test trials than observers of downward movement. These findings provide the first demonstration of which the authors are aware that birds are able not only to detect and respond to a moving video image but also to copy its movements.

Imitation, copying the motor patterns of others, is a variety of social learning that is thought to be special in terms of its psychological mechanisms and its potential to support cultural transmission of behavior (Galef, 1988; Heyes, 1993; Heyes & Galef, 1996). Recent research using the two-action test has provided evidence of imitation in several species of bird (e.g., Japanese quail: Akins, Klein, & Zentall, 2002; Dorrance & Zentall, 2001; European starlings: Campbell, Heyes, & Goldsmith, 1999; Fawcett, Skinner, & Goldsmith, 2002). In a two-action test, observers are first exposed to a demonstrator operating on a single object in one of two different ways. Then, each observer is given access to the object and a record is made of the number of times the observer manipulates it using the same action as the demonstrator and using the alternative action, the one that was not observed. A bias in favor of the former, demonstrator-consistent responding, implies that the subjects copied one or both of the observed actions.

Two-action tests for imitation in budgerigars have had mixed results. Dawson and Foss (1965) reported that budgerigars would copy the method used by a demonstrator to remove a flat, square

cover from a food cup; the methods of removal were classified as "edged off by the beak," "lifted off by the beak," or "used foot to dislodge the square." Several attempts to replicate this effect have failed (R. A. Boakes, personal communication, July 2001; Galef, Manzig, & Field, 1986; Moore, 1992), and in the only reported successful replication, Galef et al. (1986) found the effect to be of brief duration and marginal significance. However, using a different procedure, Heyes and Saggerson (2002) found that budgerigars would copy an upward or downward movement used by demonstrators to remove a stopper from a food box and that this effect, which was detected on the first occasion when the observers removed the stopper, persisted over at least 24 test trials.

Problems with stimulus control are likely to have contributed to lack of reliability of the Dawson and Foss (1965) effect and of social learning phenomena more generally. In social learning experiments, it is usually the demonstrator animal, whose priorities may be rather different from those of the experimenter, that controls stimulus presentation. In their study of imitation in budgerigars, Galef et al. (1986) noted that there was substantial variability between demonstrators in the method used to remove the food cover and that they were largely powerless to control this variation. With the intention of developing a technique that could overcome such problems, the present study used video playback; we sought evidence that budgerigars will copy virtual rather than live demonstrators. There are many potential advantages associated with video playback. The experimenter is able to control the timing of demonstrations, and an identical stimulus demonstration can be presented repeatedly to the same and/or different animals (D'Eath, 1998). Furthermore, sequences of events can be manipulated, such that objects and/or their movements can be hidden or added, and the relative timing of events can be changed (e.g., Morimura & Matsuzawa, 2001).

A number of studies have shown that birds can discriminate between objects presented in video images (for reviews, see D'Eath, 1998; Lea & Dittrich, 1999), but research on social learning using this technology has not been uniformly successful. For example, there is evidence that hens have difficulty discriminating between video images of conspecifics (D'Eath & Dawkins, 1996;

Patterson-Kane, Nicol, Foster, & Temple, 1997). However, in a promising study, McQuoid and Galef (1993) found that when red junglefowl chicks are offered a choice of two colored dishes from which to feed, they prefer the dish from which they have seen a conspecific feeding in video playback.

Some of the negative results of previous video playback research may have been due to the use of cathode ray tube displays. The eyes of fast-moving animals such as birds, bees (Lythgoe, 1979), spiders (Clark & Uetz, 1990, 1992, 1993), and certain fish (Ali & Klyne, 1985) have evolved the ability to process visual information (e.g., such as the flickering of a light) into stable images at much higher critical flicker-fusion frequencies than many mammals. Humans have a maximum critical flicker-fusion frequency of 60 Hz, which is much lower than that of some birds (e.g., domestic hens, 105 Hz: Nuboer, Coemans, & Vos, 1992; pigeons, 140 Hz: Dodt & Wirth, 1953; African grey parrots, 55.3–105 Hz: Nuboer et al., 1992). This discrepancy can result in a video image that may appear flicker free to the experimenter but distorted to birds. In the present study, we elected to use thin film transistor (TFT) liquid crystal displays that do not produce this distortion. TFT displays of virtual female models have been shown to generate responses from male zebra finches and Bengalese finches comparable with those obtained with live females. Cathode ray tube displays of the same females generated almost no response (Ikebuchi & Okanoya, 1999). Furthermore, it has recently been shown that female Japanese quail affiliate with live males after seeing them mate in a TFT video display (Ophir & Galef, 2003).

The naive observer budgerigars in the present experiments observed video playback of a conspecific demonstrator repeatedly removing a blue stopper from the horizontal surface of a white food box, either by pulling the stopper up or by pushing it down into the box, and then feeding from within. During (Experiment 1) or after (Experiment 2) each demonstration period, the observer was given access to two stoppers (one blue and one black) and rewarded with access to food for the removal of either stopper in either direction. A reliable bias in favor of using the same upward or downward removal method as the demonstrator when manipulating either stopper would suggest that the observers had copied the up method, the down method, or both. To distinguish these possibilities, we added a control group to the basic two-action design used by Campbell et al. (1999) and Heyes and Saggerson (2002). Control birds observed a virtual demonstrator feeding through the hole normally occupied by the blue stopper but did not see the blue stopper or the action of stopper removal. If the directional bias of the control birds is intermediate between those of the other two groups, it would suggest that both up observers and down observers copy their virtual demonstrators. Two stoppers were used in the present experiment to make the procedure as similar as possible to that used by Heyes and Saggerson with live budgerigar demonstrators. However, given that both experimental groups saw the blue stopper manipulated and that the controls saw a virtual demonstrator feeding at the site where the blue stopper was located on test, we did not anticipate any differences between groups in the proportion of removal responses directed toward the two stoppers.

Experiment 1: Simultaneous Observation and Testing

McQuoid and Galef (1993) found that in Burmese jungle fowl social learning from video playback is sensitive to the interval between observation and testing. To maximize the chances of finding an effect of virtual demonstrator observation on direction of stopper removal, in our first experiment we set this interval to zero by allowing birds to observe video playback and to remove stoppers simultaneously.

Method

Subjects. Eleven male budgerigars (*Melopsittacus undulatus*) of indeterminate age (but at least 3 months old) were used in the experiment: 2 demonstrators and 9 observers. The demonstrators had fulfilled the same role in a previous study (Heyes & Saggerson, 2002), and the observers were experimentally naive. All birds were obtained from a commercial supplier and allowed to habituate to laboratory conditions for at least 1 week prior to the experiment. Observers and demonstrators were housed in separate groups in metal panel and galvanized wire mesh cages (0.5 m × 0.5 m × 1.0 m). They had ad libitum access to water at all times. During the experiment, the birds were weighed daily and maintained at no less than 90% of free-feeding body weight through the provision of 3–6 g of millet seed per bird after each daily session. At all other times birds were fed ad libitum on standard parakeet seed mix. In addition, cuttlebone, mineral blocks, oyster shell bits, and spray millet were available. The holding room was maintained on a 12-hr light–dark cycle (light onset at 0800) at 21 ± 2 °C.

Apparatus. The birds were trained and tested in the holding room in a commercially supplied parakeet wire mesh cage (58 cm × 32 cm × 41 cm) lined with newspaper, which served as the test chamber (see Figure 1). The wire mesh was removed at one end of the cage and replaced with clear Plexiglas to enable birds to view a computer screen (details below) located outside the cage. A removable opaque wooden blind was located 15 cm from the other end of the cage. The area between the Plexiglas screen and the blind was used for observation and testing, whereas the area between the blind and the other end of the cage served as a holding area for observers before testing and between trials. The holding area contained two plastic perches.

A white, rectangular aluminum box (21 cm × 10 cm × 5 cm) with a white plastic lid was located on the floor of the observation–test compartment with its long axes adjacent to and in the center of the Plexiglas wall. This stopper box contained standard parakeet mix in a layer 1–2 cm deep and had two 3.4-cm holes in its lid. The holes were 7.0 cm apart, 4.0 cm from the ends of the box, and 3.5 cm from the sides. At various points in the experiment (specified below), the holes were blocked by two stoppers, one blue and the other black. Two strands of metal wire (1 mm thick), arranged in a rigid cross spanning the upper, concave surface of each stopper, could be gripped by the birds. The blue stopper was always in the left hole and the black stopper in the right hole with respect to a bird approaching from the far end of the test cage. A perch was located 2 cm away from the stopper box and 5 cm above the floor.

Outside the test chamber, the 20 cm TFT screen of a Pentium laptop computer was aligned approximately parallel to and 15 cm from the Plexiglas wall. Subjects were viewed and recorded via closed circuit television located on a stand below the apparatus and an analog 8-mm Sony camcorder placed either directly above or on a tripod to the side of the apparatus. The equipment was controlled and the data were collected manually by the experimenter (Kieron Mottley), who was positioned approximately 0.5 m from the back of the test chamber on the side furthest from the cage door. This side of the chamber and the end wall made of mesh (rather than Plexiglas) were covered on the outside by opaque black plastic sheeting to ensure that the experimenter was not visible to the birds during training and testing.
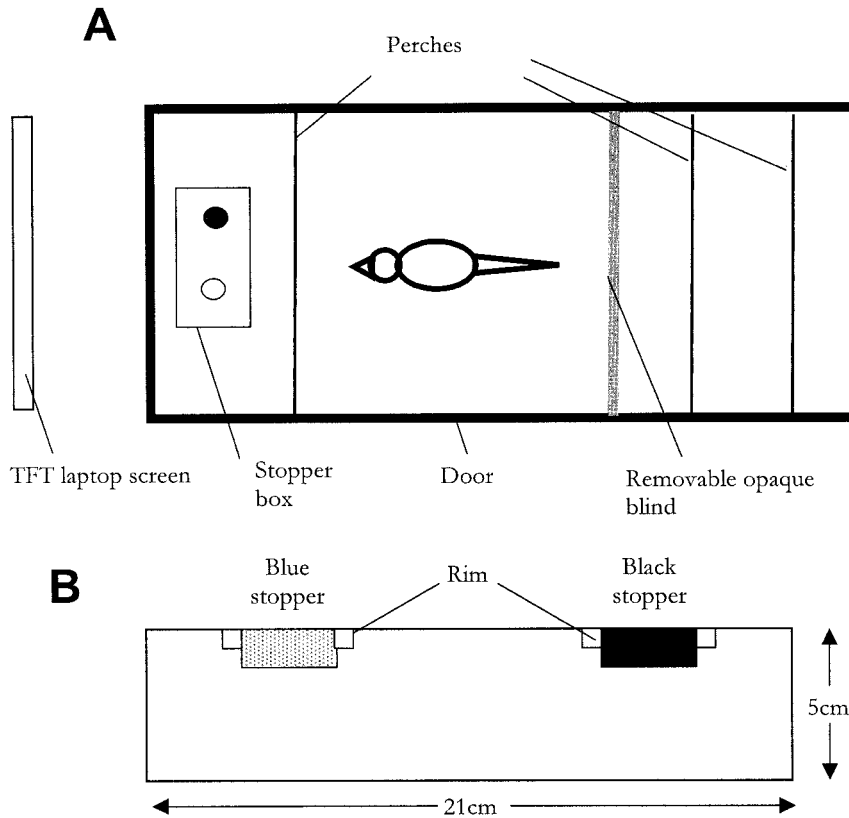
Figure 1. A: Plan of the apparatus used in Experiments 1 and 2. B: Cross section of the stopper box. The stoppers were either pulled up from the surface of the box or pushed down into the box. TFT = thin film transistor.

Stimuli. In a previous experiment, 1 of the demonstrator birds had been trained to remove stoppers by pulling upward, and the other had been trained to remove stoppers by pushing them downward into the box (see Heyes & Saggerson, 2002, for details of demonstrator training). Footage of these birds, recorded using a Canon miniDV digital camcorder, was translated into digital movie files and edited to produce three sequences that were used in the main experiment: up, down, and control. The up sequence showed a demonstrator alight on the lid of the stopper box, bend its head to grasp in its beak a cross-wire on the blue stopper, jerk its head upwards, and throw the stopper off screen. The down sequence also began with the demonstrator alighting on the stopper box and grasping a cross-wire on the blue stopper in its beak. However, in this case, gripping the wire was followed by a sharp downward thrust of the beak that caused the stopper to move into the box, where it disappeared from view. In both the up and down sequences, stopper removal took approximately 2 s and was followed by 10 s in which the demonstrator could be seen feeding from the box. The control sequence showed a demonstrator feeding from the box for 10 s through the hole where the blue stopper was located in the up and down sequences but not stopper removal. A fourth sequence, showing both demonstrator birds simultaneously feeding through the two holes in the stopper box, was used during magazine training. The stoppers were not visible in this sequence.

In all sequences, the images were life-size, showed the stopper box in the position it occupied during observer testing, and were filmed with the camera facing in the same direction as an observer bird approaching the stopper box from the holding area. Throughout each sequence, the demonstrator birds were facing the camera or shown in profile. The camera angle was approximately 60° with respect to the upper surface of the

stopper box, and the whole box was included in the frame so that the immobile black stopper was visible in the up, down, and control sequences. The same sequence of recorded sounds was played in conjunction with each of the visual sequences. This common, auditory sequence was produced by playing simultaneously the soundtracks recorded during filming of the up, down, and control visual sequences. It consisted of scratching sounds and budgerigar calls and was played at a low volume, just audible to the human ear.

Procedure. All training and testing was conducted in the afternoon and evening and timed to coincide with the end of the light phase of the birds' light–dark cycle. The 9 observer birds were randomly assigned in equal numbers to one of the three groups: up, down, and control. Prior to virtual demonstrator observation, the observers were habituated to the test apparatus and procedure and trained to feed through the holes in the lid of the stopper box in eight daily magazine training sessions. The stoppers were absent during these sessions. On Days 1–3 of magazine training, each bird spent 5 min in the test cage, and at the end of Day 3, each bird was placed on a feeding schedule. On Days 4–8, each bird was given five trials in which it was released from the holding area, allowed to approach and feed from the stopper box for 30 s, and then ushered back to the holding area where the blind was replaced. If a bird did not feed, the trial ended after 1 min. During these trials, the video sequence of 2 birds feeding from the stopper box was playing continuously on the computer screen.

The day after the last magazine training session, the birds began seven daily sessions of observation and testing, each consisting of seven trials. These trials were the same as the magazine training trials on Days 4–8 except that the stoppers were in place and either the up, down, or control sequence was replaying continuously on the computer screen. Thus, in

each observation–testing session, the birds had seven opportunities to remove the blue or black stopper while observing the virtual demonstrator repeatedly removing the blue stopper using an upward motion (up group) or a downward motion (down group), or feeding through the hole where the blue stopper was normally located (control group). Whenever an observer removed a stopper, regardless of whether an upward or a downward movement was used, it was allowed to feed through the hole in the box for 30 s. This interval was timed carefully with a stopwatch to ensure that birds were not inadvertently given a longer period to feed after demonstrator-consistent responses than after demonstrator-inconsistent responses. Thus, the observers were not trained by differential reinforcement to use the same movement as their demonstrators. There was an interval of approximately 5 s between each trial in which the experimenter replaced the stopper removed by the observer bird.

If a bird did not remove a stopper and feed on two consecutive trials, it was given an additional trial (without video playback) in the absence of the stoppers and allowed to feed from the box for 10 s. These additional trials, which did not count toward the bird's total of seven per session, were designed to motivate the observer by "reminding" it that food was available in the box. The order in which birds were tested each day was randomized across groups to control for time of day.

Videotapes of the observers' behavior during test trials were scored by two independent raters, one of whom was blind to the viewed birds' group assignment. Whenever an observer removed a stopper using its beak and fed from the box, the raters recorded the direction of movement (up or down) and the color (blue or black) of the stopper. The raters were in agreement regarding the direction and color of stopper removal in 99.8% of a randomly selected 30% of test trials. Directional discrimination ratios, calculated by dividing the number of up removal responses by the total number of removal responses, were used to assess whether observers tended to remove the stopper in the same direction as their virtual demonstrator. Color discrimination ratios, calculated by dividing the number of blue removals by the total number of removals, were used to assess any object preferences.

Test sessions were scored relative to the observer's performance. For example, "Test 1" refers to the first test session in which a bird made a response, whether or not this was the first test session administered. This method of organizing the data allows examination of how, if at all, effects of conspecific observation change as observers gain experience of direct interaction with the apparatus, that is, with increasing opportunity for individual learning.

Results and Discussion

The topographies of observers' removal responses were similar to those of the demonstrators. While standing on the lid of the box, the bird moved its head toward the stopper. For an up response, the mandibles were then closed on the cross-wire, and the head was pulled sharply upward. The stopper, which was released at the zenith of the upward movement, then landed either on the upper surface of the box, on the cage floor, or on the floor of the stopper box. For down responses, the mandibles were closed on the cross-wire, and a downward thrust of the head caused the stopper to fall downward onto the floor of the stopper box.

Owing to the small sample size, it was not possible to assess whether the data were normally distributed, and therefore they were subjected to nonparametric analysis using Kruskal–Wallis one-way analysis of variance (ANOVA) by ranks. All tests were two-tailed, unless stated otherwise. Conventionally, an alpha value of .05 was applied.

On average, each bird made 31.33 ($SEM = 4.38$) removal responses in total and was given a total of 3.22 ($SEM = 0.89$) additional trials across all seven test sessions. The groups did not

differ on either of these measures: total removal responses, $H(2) = 3.96$; additional trials, $H(2) = 3.01$. One bird, in the down group, failed to respond in the first test session administered, and therefore, for this bird, the session analyzed as Test 1 was the second test administered.

Analysis of color discrimination ratios suggested that the up group ($M = .60$, $SEM = .28$) and the down group ($M = .47$, $SEM = .21$) removed the blue stopper proportionally more often than the control group ($M = .04$, $SEM = .02$), but the effect of group was not reliable, $H(2) = 3.29$. Thus, there was no evidence that the birds were biased in favor of responding to the stopper of the same color and at the same location as that of their virtual demonstrators.

Figure 2 shows the data of principal interest, the mean directional discrimination ratio for each group calculated across removals of both stoppers. A nonparametric ANOVA indicated a significant effect of group, $H(2) = 7.20$, exact $p = .004$, and subsequent pairwise comparisons (Siegel & Castellan, 1988, p. 213) confirmed that observers of up responding made a greater proportion of up responses than observers of down responding (difference in mean rank = 6, critical difference $Z = 5.35$). The differences between the up and control groups and between the down and control groups were not reliable (difference in mean rank = 3, in both cases).

In addition to removing stoppers with their beaks, the observers sometimes displaced a stopper downward with their feet as they walked over the top of the box. This kind of displacement, which appeared to be accidental, occurred on average 12.22 ($SEM = 3.30$) times across the seven test sessions. When these displacements were scored as down responses, the pattern of results was unchanged: There was a reliable effect of group, $H(2) = 5.96$, exact $p = .025$, and a marginally significant difference between the up and down groups (difference in mean rank = 5.33).

One control subject and 2 birds in the down group failed to respond in all seven tests, and therefore, the sample sizes at each
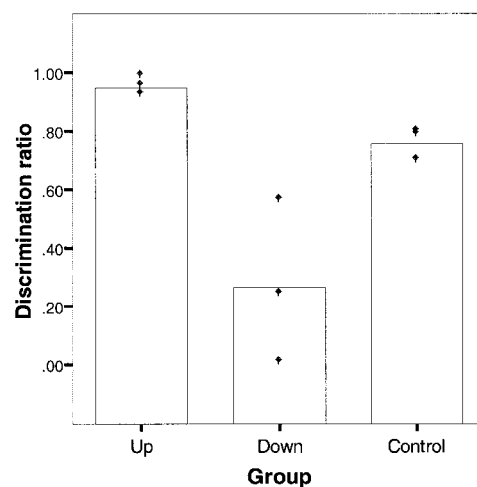

Figure 2. Bars show mean directional discrimination ratios (calculated by dividing the number of up removal responses by the total number of removal responses) across all test sessions for the up, down, and control groups in Experiment 1 (simultaneous observation and testing). Points represent individual birds.

of Tests 5–7 were too small for analysis of how the observers' response biases developed across test sessions.

Thus, the results of Experiment 1 indicate that birds that had observed a virtual demonstrator removing a stopper from a food box using an upward motion made proportionally more up responses than birds that had observed a virtual demonstrator using a downward motion.

Experiment 2: Successive Observation and Testing

The results of Experiment 1 suggest that when observation and testing are simultaneous, budgerigars will copy the action used by a virtual demonstrator to remove a stopper from a food box. This is a striking outcome, but it has three limitations: First, Experiment 1 involved a small sample of birds, and therefore, although statistically significant, the effects may have been due to sampling error. Second, because observation and testing were simultaneous, it is possible that instead of receiving and storing some information from the virtual demonstrator, the observers merely reacted to stimuli immediately present on the screen. For example, observers may have simply tracked demonstrator head movements with their own heads (D'Eath & Dawkins, 1996). Third, Experiment 1 did not establish whether budgerigars copy upward movements, downward movements, or both. The directional bias of control birds was numerically, but not statistically, intermediate between those of up and down observers. To overcome these limitations, we replicated the basic procedure used in Experiment 1 in Experiment 2 with a larger sample of birds and with successive observation and testing. Thus, on each trial in Experiment 2, observers were first allowed to observe a virtual demonstrator and then returned to the holding area before being given access to the stopper box when the computer screen was blank.

Method

The method used in Experiment 2 differed from that of Experiment 1 in three respects. (a) Twenty-four naive budgerigars were randomly assigned in equal numbers to up, down, and control groups. (b) Each trial consisted of a 1 min period of virtual demonstrator observation, while the stopper box was covered by a sheet of white cardboard, followed approximately 5 s later by a 1 min test period that was identical to that of Experiment 1 except that the computer screen (37-cm TFT) was blank. Between observation and testing, the observer was confined in the holding area. (c) The up, down, and control video sequences each consisted of three different takes of the demonstrator, in continuous rotation. The topography of the demonstrator's behavior was substantially the same in each take, but it was thought that the small variations between takes in, for example, the angle of the demonstrator's approach to the stopper box might help to sustain the observers' attention.

Results and Discussion

Two birds in the control group failed to respond in the first two test sessions and, because they were showing signs of illness, were excluded from further testing. One bird in the up group repeatedly knocked a stopper into the box with its foot but never made a removal response with its beak. Therefore, for the purposes of analysis, the sample sizes for the groups were as follows: up, $n = 7$; down, $n = 8$; and control, $n = 6$. Observers' response topographies were the same as those reported in Experiment 1.

Preliminary analysis using Levine's test indicated that when they were pooled across test sessions, the data from Experiment 2 showed equality-of-error variances across groups. Therefore, parametric one-way ANOVA was applied to these data.

On average, each bird made 32.20 ($SEM = 3.78$) removal responses in total, and the groups did not differ in this respect, $F(2, 18) = 1.22$, $p > .05$. No bird in Experiment 2 was given additional trials. Two birds, one in the down group and the other in the control group, failed to respond in the first test session administered. For these birds, the session analyzed below as Test 1 was the second test administered.

The mean color discrimination ratios were .57 for the up group ($SEM = .20$), .56 for the down group ($SEM = .17$), and .42 for the control group ($SEM = .20$; $F < 1$). Thus, as in Experiment 1, the observers did not show an overall bias in favor of responding to one of the two stoppers.

Mean directional discrimination ratios for responses to both stoppers are presented in Figure 3. There was a significant effect of group, $F(2, 18) = 3.38$, $p = .057$, and post hoc comparisons confirmed that the up group made proportionally more up responses than the down group ($p = .048$). On average, the observers displaced a stopper by walking over it 13.86 ($SEM = 3.69$) times in the course of testing. The results were the same when these displacements were scored as down responses; the effect of group, $F(2, 18) = 4.60$, $p = .024$, and the difference between the up and down groups ($p = .027$) were reliable.

Of the 15 birds in the up and down groups, 12 made more than 50% of their beak responses in the same direction as their demonstrator, $\chi^2(1, N = 15) = 5.40$, $p = .05$. Similarly, when displacements with the foot were counted as down responses, 13 of the 15 birds made a majority of their responses in the demonstrator-consistent direction, $\chi^2(1, N = 15) = 8.07$, $p = .006$.

Preliminary analysis of directional discrimination ratios for each test session indicated that in later sessions those of the up and
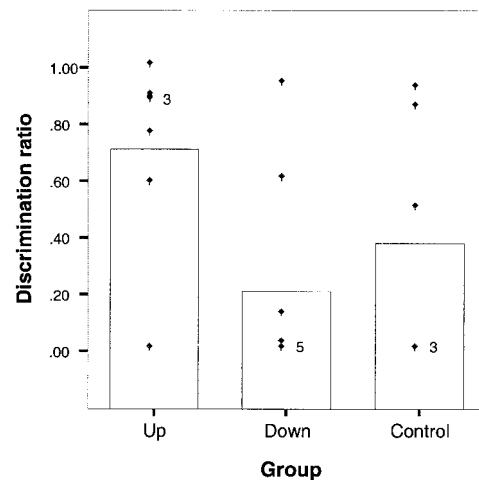

Figure 3. Bars show mean directional discrimination ratios (calculated by dividing the number of up removal responses by the total number of removal responses) across all test sessions for the up, down, and control groups in Experiment 2 (successive observation and testing). Points represent individual birds. Numbers beside some points indicate the number of birds with that ratio value.

down groups were predominantly 1 or 0; that is, each bird removed stoppers using an upward or a downward movement exclusively. Thus, the scores were not normally distributed and therefore could not be subjected to parametric analysis. To facilitate nonparametric analysis of the influence of the virtual demonstrator across test sessions, we categorized the performance of each bird in each test according to whether its directional discrimination ratio was greater or less than .5 (a score of .5 was not obtained in any test session). Figure 4 shows for each test session the percentage of the birds in each group that made more than half of their removal responses in the up direction (i.e., with ratios greater than .5). Inspection of this figure suggests that observers of up responding, but not observers of down responding or control birds, made proportionally more up responses across test sessions, as they gained more experience of direct interaction with the apparatus. Wilcoxen signed-ranks analysis confirmed that in the up group, more birds made a majority of up responses in Tests 4–7 than in Tests 1–3 ($Z = 2.07$, $p = .038$), whereas in the down and control groups, the number of birds making more up than down responses did not increase over tests ($Z = 0.45$, in both cases). Furthermore, whereas observers of up and down responding did not differ in Tests 1–3 (Mann–Whitney $U = 17$), more birds in the up group than in the down group made a majority of up responses in Tests 4–7 ($U = 5$, $p = .015$).

Thus, like Experiment 1, Experiment 2 replicated with virtual demonstrators the directional matching effect previously found by Heyes and Saggerson (2002) with live budgerigar demonstrators: Observers of up responding made a greater proportion of up responses than observers of down responding, and the former group did, whereas the latter did not, show an increasing bias toward up responding over test sessions. The occurrence of this matching effect in Experiment 2 indicates that it does not depend on simultaneous observation and testing and thereby that it is unlikely to be due to visual tracking of the virtual demonstrator's movements.
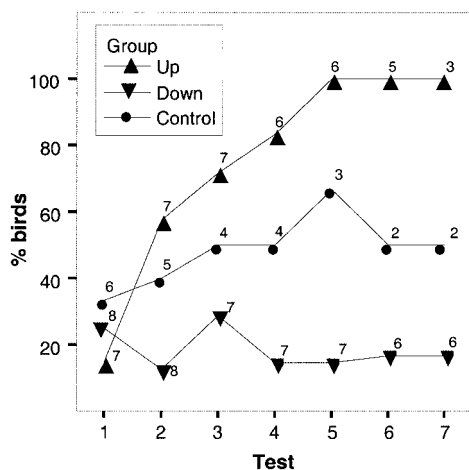

Figure 4. Percentage of birds in the up, down, and control groups that made more up than down removal responses at each test session in Experiment 2. Sample size values are given alongside each data point. These decline over tests because some birds responded in fewer than seven test sessions.

The directional bias of control birds was similar to that of up observers in Experiment 1 and to that of down observers in Experiment 2. When directional discrimination ratios based on all removal responses in both experiments were combined in one analysis, the main effect of experiment, $F(1, 24) = 2.15$, and the Experiment $\times$ Group interaction, $F(2, 24) = 1.10$, were not reliable, but there was a significant main effect of group, $F(2, 24) = 7.93$, $p = .002$. Simple contrast analysis confirmed the predictions that the up group would show a stronger up bias than the control group ($p = .03$, one-tailed) and that the down group would show a weaker up bias than the control group ($p = .032$, one-tailed).

General Discussion

In both of the experiments reported here, birds that observed a virtual demonstrator removing a stopper from a food box using an upward or a downward movement showed a reliable bias in favor of using the same method of stopper removal themselves. This implies that budgerigars will copy not only live demonstrators (Heyes & Saggerson, 2002) but also video playback of demonstrator action. Previous research has shown that video playback of a feeding and an active nonfeeding conspecific has differential effects on feeding-site selection in Burmese jungle fowl (McQuoid & Galef, 1993). The present findings suggest a yet more subtle effect: that budgerigars respond differentially to video playback of two different foraging behaviors at the same site and that they gain sufficient information from virtual demonstration to enable them to reproduce the act observed.

The directional biases of up and down observers differed when observation and testing were successive (Experiment 2) as well as when they were simultaneous (Experiment 1), suggesting that the effect is due to social learning rather than to the observers tracking, or moving in phase with, the demonstrator's movements. However, the present data could be due to social learning about object movements or about body movements. The birds may have learned by observation that an upward or downward trajectory of the stopper predicted the sight of food or a feeding conspecific, or they might have learned by observation to remove stoppers with an up or down thrust of the head and mandibles. The results of most two-action tests are open to these explanations, and therefore, developing techniques to distinguish them is currently a priority in primate (Heyes, 2001; Stoinski, Wrate, Ure, & Whiten, in press; Voekl & Huber, 2000; Whiten, 1998) as well as avian research on social learning. Because they allow independent manipulation of the object and action components of an image, video playback procedures could make a valuable contribution to this endeavor.

Byrne (2002) has suggested that demonstrator-consistent behavior in two-action tests provides evidence of "response facilitation"; that is, "observation results in the priming of brain records of motor behavior" (p. 83). Whether they are described as response facilitation or imitation, the results of two-action tests challenge psychologists to find out why and how observation produces matching behavior. This is a significant problem because matching behavior, that which resembles the demonstrator's when viewed from a third party perspective, may give rise to very different sensory inputs when observed and executed. For example, the visual input to a budgerigar observing stopper removal includes upward or downward movement of the demonstrator's whole

body, but when a bird executes both of these actions, it cannot see the outline of its whole body, and the stopper dominates the visual field. More generally, it is not clear on which perceptual dimensions, if any, there is a greater similarity between observing and performing upward stopper removal than between observing upward removal and performing a downward response.

The comparison between the up and down groups fulfilled the principal purpose of the present study by establishing that budgerigars will copy the behavior of a virtual demonstrator. In accordance with the basic logic of the two-action test, a difference between the directional biases of these two groups implies that one or both of them copied observed movement. The control group was included to address the subsidiary question of whether budgerigars copy video playback of up responding, down responding, or both. The results did not provide a clear answer to this question because the directional preferences of the control birds varied between experiments. They showed a bias toward up removal in the first experiment and down removal in the second. It is possible that control birds show greater variability in their directional preferences than observers because the control birds' behavior is not channeled or guided by conspecific observation. In this case, sampling error alone could have been responsible for the variation across experiments in the control birds' directional preferences. Some support for this hypothesis was provided by the combined analysis of data from Experiments 1 and 2, which increased the control sample size and indicated reliable differences between each of the three groups. Thus, the results of the present study support the tentative conclusion that budgerigars can copy upward and downward removal methods from a virtual demonstrator and suggest that when control groups are added to two-action designs, they should include relatively large numbers of subjects.

Foraging site selection was not a focus of the present study, and we did not anticipate any differences between groups in the distribution of removal responses across the blue and black stoppers because all three groups observed activity directed toward the blue stopper (up and down groups) or at the location occupied by the blue stopper on test (control group). However, it is somewhat surprising that across groups the birds did not show a preference for the blue stopper. Stimulus enhancement effects, in which an observer focuses its activity on an object or at a location associated with demonstrator behavior, have been found in a range of species and procedures (e.g., Hare & Tomasello, 1999; Itakura, Agnetta, Hare, & Tomasello, 1999), including a paradigm similar to the present one, in which birds were exposed to videotapes of demonstrator behavior. McQuoid and Galef (1993) found that Burmese jungle fowl that had seen and heard a virtual demonstrator feeding from a dish marked with either blue or red subsequently preferred to feed from a dish with markings of the same color.

Several differences between our procedure and that used by McQuoid and Galef (1993) are likely to have prevented detection of a stimulus enhancement effect in Experiments 1 and 2. First, red and blue may be more discriminable for birds than blue and black. Second, because the present study was looking for copying of removal method, rather than of activity site, we did not vary the locations of the stoppers on test, and the blue stopper was always located on the more exposed side of the test cage. It was adjacent to the door and closer to the cage wall that was open rather than covered with black plastic. Third, whereas McQuoid and Galef's birds were magazine trained with unmarked dishes, the observers

in Experiments 1 and 2 learned during magazine training that food was available at both response locations. Fourth, the birds in the previous study were exposed to only one of the discriminative stimuli during observation, the red or the blue markings, but in our demonstration sequences the black stopper was continuously present, and the blue stopper was either absent (control group) or swiftly removed from the shot by the demonstrator (up and down groups). Thus, the observer budgerigars had more opportunity to habituate to the black stopper than to the blue one. Finally, in McQuoid and Galef's study, either 10 min or 48 hr elapsed between observation and testing, but in the present experiments, the virtual demonstrator was present either during testing (Experiment 1) or no more than 1 min before and after each test trial (Experiment 2). Consequently, the observers may sometimes have selected the black stopper, the one at a greater distance from the demonstrator, to avoid feeding competition.

Returning, in conclusion, to the focus of the present study, our results indicate that budgerigars will copy foraging movement of a virtual demonstrator. As far as we are aware, this is the first demonstration that birds are capable not only of detecting and responding to a dynamic video image but also of copying its movements. This finding will help to overcome the problems of stimulus control inherent in research on social learning and may prove to have substantial implications in developing psychologists' understanding of visual perception and motor control in animals.

References

Akins, C. K., Klein, E. D., & Zentall, T. (2002). Imitative learning in Japanese quail using the bidirectional control procedure. *Animal Learning & Behavior, 30,* 275–281.

Ali, M. A., & Klyne, M. A. (1985). *Vision in vertebrates.* New York: Plenum Press.

Byrne, R. W. (2002). Imitation of novel complex actions: What does the evidence from animals mean? *Advances in the Study of Behavior, 31,* 77–105.

Campbell, F. M., Heyes, C. M., & Goldsmith, A. R. (1999). Stimulus learning and response learning by observation in the European starling, in a two-object/two-action test. *Animal Behaviour, 58,* 151–158.

Clark, D. L., & Uetz, G. W. (1990). Video image recognition by the jumping spider. *Animal Behaviour, 40,* 884–890.

Clark, D. L., & Uetz, G. W. (1992). Morph-dependent mate selection in a dimorphic jumping spider: Demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour, 43,* 247–254.

Clark, D. L., & Uetz, G. W. (1993). Signal efficacy and the evolution of male dimorphism in the jumping spider. *Proceedings of the National Academy of Sciences, USA, 90,* 11954–11957.

Dawson, B. V., & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour, 13,* 470–474.

D'Eath, R. B. (1998). Can video images imitate real stimuli in animal behaviour experiments? *Biological Review, 73,* 267–292.

D'Eath, R. B., & Dawkins, M. S. (1996). Laying hens do not discriminate between video images of conspecifics. *Animal Behaviour, 52,* 903–912.

Dodt, E., & Wirth, A. (1953). Differention between rods and cones by flicker electroretinography in pigeon and guinea pig. *Acta Physiologia Scandinavica, 30,* 80–89.

Dorrance, B. R., & Zentall, T. R. (2001). Imitative learning in Japanese quail (*Coturnix japonica*) depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology, 115,* 62–67.

Fawcett, T. W., Skinner, A. M., & Goldsmith, A. R. (2002). A test of imitative learning in starlings using a two-action method with an enhanced ghost control. *Animal Behaviour, 64,* 547–556.

Galef, B. G. (1988). Imitation in animals: History, definition and interpretation of data from the psychological laboratory. In T. R. Zentall & B. G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale, NJ: Erlbaum.

Galef, B. G., Manzig, L. A., & Field, R. M. (1986). Imitation learning in budgerigars: Dawson and Foss (1965) revisited. *Behavioral Processes, 13,* 191–202.

Hare, B., & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology, 113,* 173–177.

Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour, 46,* 999–1010.

Heyes, C. M. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences, 5,* 253–261.

Heyes, C. M., & Galef, B. G. (Eds.). (1996). *Social learning in animals: The roots of culture.* San Diego, CA: Academic Press.

Heyes, C. M., & Saggerson, A. (2002). Testing for imitative and non-imitative social learning in the budgerigar using a two-object/two-action test. *Animal Behaviour, 64,* 851–859.

Ikebuchi, M., & Okanoya, K. (1999). Male zebra finches and Bengalese finches emit directed songs to the video images of conspecific females projected onto TFT display. *Zoological Science, 16,* 63–70.

Itakura, S., Agnetta, B., Hare, B., & Tomasello, M. (1999). Chimpanzee use of human and conspecific social cues to locate hidden food. *Developmental Science, 2,* 448–456.

Lea, S. E. G., & Dittrich, W. H. (1999). What do birds see in moving video images? *Current Psychology of Cognition, 18,* 765–803.

Lythgoe, J. N. (1979). *The ecology of vision.* Oxford, England: Clarendon Press.

McQuoid, L. M., & Galef, B. G. (1993). Effects of access to food during training on social learning by Burmese red junglefowl. *Animal Behaviour, 46,* 13–22.

Moore, B. R. (1992). Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour, 122,* 231–263.

Morimura, N., & Matsuzawa, T. (2001). Memory of movies by chimpanzees. *Journal of Comparative Psychology, 115,* 152–158.

Nuboer, J. F. W., Coemans, M. A., & Vos, J. J. (1992). Artificial lighting in poultry houses: Do hens perceive the modulation of fluorescent lamps as flicker? *British Poultry Science, 33,* 123–133.

Ophir, A. G., & Galef, B. G. (2003). Female Japanese quail affiliate with live males after seeing them mate on video: Transfer from moving video images to objects they represent. *Animal Behaviour, 66,* 369–375.

Patterson-Kane, E., Nicol, C. J., Foster, T. M., & Temple, W. (1997). Limited perception of video images by domestic hens. *Animal Behaviour, 53,* 951–963.

Siegel, S., & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences* (2nd ed.). New York: McGraw-Hill.

Stoinski, T. S., Wrate, J. L., Ure, N., & Whiten, A. (in press). Imitative learning by captive western lowland gorillas in a simulated food-processing task. *Journal of Comparative Psychology.*

Voekl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour, 60,* 195–202.

Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 112,* 270–281.

New Editor Appointed for *Contemporary Psychology: APA Review of Books,* 2005–2010

The Publications and Communications Board of the American Psychological Association announces the appointment of Danny Wedding (Missouri Institute of Mental Health) as editor of *Contemporary Psychology: APA Review of Books,* for a 6-year term beginning in 2005. The current editor, Robert J. Sternberg (Yale University), will continue as editor through 2004.

All reviews are written by invitation only, and neither the current editor nor the incoming editor receives books directly from publishers for consideration. Publishers should continue to send three copies of books for review consideration, along with any notices of publication, to PsycINFO Services Department, APA, Attn: *Contemporary Psychology: APA Review of Books* Processing, P.O. Box 91600, Washington, DC 20090-1600 or (for UPS shipments) 750 First Street, NE, Washington, DC 20002-4242.