Testing for imitative and nonimitative social learning in the budgerigar using a two-object/two-action test

CECILIA HEYES & ANNA SAGGERSON

Department of Psychology, University College London

Male and female juvenile budgerigars, *Melopsittacus undulatus*, were allowed to observe a conspecific demonstrator using its beak to remove one of two distinctively coloured objects (i.e. a blue and a black stopper) from a hole in the lid of a box and eating seed from within. Both objects could be removed by either pulling up or pushing down. When subsequently allowed access to both stoppers, and rewarded with food for all removal responses, regardless of the object to which they were made and their direction, observer birds removed both stoppers in the same direction as their demonstrator. This effect was present on the first occasion when observers removed a stopper, and persisted over at least 24 trials. Female observers made more removal responses than males, but conspecific observation had equivalent effects on direction of responding in males and females. All observers tended to approach the same object as their demonstrator when the objects were discriminable using both spatial and colour cues, but not when they differed in colour alone. Contrary to previous findings, these results suggest that robust behavioural matching effects can be obtained in budgerigars, and that these birds are capable of motor imitation or emulation.

Recent evidence challenges the longstanding assumption that, while some show vocal imitation, birds are incapable of motor imitation (e.g. Thorndike 1898). Evidence of motor imitation, defined as copying by an observer of a novel feature of the body movement of a demonstrator (Heyes 2001), has been found in pigeons, *Columbia livia* (Zentall et al. 1996; Kaiser et al. 1997), Japanese quail, *Coturnix japonica* (Akins & Zentall 1996, 1998; Dorrance & Zentall 2001; Akins et al., in press), Carib grackles, *Quiscalus lugubris* (Lefebvre et al. 1997), ravens, *Corvus corax* (Fritz & Kotrschal 1999) and European starlings, *Sturnus vulgaris* (Campbell et al. 1999; Fawcett et al. 2002). Each of these studies used a two-action test designed to isolate imitation from social facilitation, in which the presence or activity of another animal promotes activity in the observer, and from non-imitative forms of social learning. In the latter, the observer performs the same body movement as the demonstrator as a result of learning by observation, not about the body movement itself, but about the environmental object to which the action was directed (Galef 1988; Heyes 1994). For example, a demonstrator's action may provide information about the static (stimulus enhancement) or dynamic (emulation) properties of a manipu-

Correspondence: C. Heyes, Department of Psychology, University College London, Gower Street, London WC1E 6BT, U.K. (email c.heyes@ucl.ac.uk).

landum, or provide the observer with an opportunity to learn that the appearance or movement of an object signals the occurrence of an appetitive or aversive event (observational conditioning).

In a two-action test, observers are first exposed to a demonstrator operating on a single object in one of two ways. Then each observer is given access to the object and a record is made of the number of times they manipulate it using the same action as their demonstrator, and using the alternative action, the one that they did not observe. A bias in favour of the former, of demonstrator-consistent responding, provides prima facie evidence of imitation; it implies that the subjects copied one or both of the observed actions.

In two-action tests, pigeons (Zentall et al. 1996), quail (Akins & Zentall 1998; Dorrance & Zentall 2001), Carib grackles (Lefebvre et al. 1997) and starlings (Campbell et al. 1999) have all shown demonstrator-consistent responding. This evidence of motor imitation in birds raises many intriguing questions. What are the psychological and neurobiological mechanisms of avian motor imitation? Are these mechanisms the same as those mediating motor imitation in human and nonhuman primates and, if so, are they homologous or analogous (e.g. Whiten 1998; Voekl & Huber 2000; Stoinski et al., in press)? What, if any, is the relationship between motor and vocal imitation in birds?

To address these questions, it would be advantageous to have a two-action test that reliably yields evidence of motor imitation in an avian species that is (1) hardy and accessible, (2) a vocal mimic and (3) well studied in terms of neuroanatomy and neurophysiology. The budgerigar, *Melopsittacus undulatus*, meets all three of these requirements. Domesticated budgerigars, which are identical in many respects to the wild budgerigars that live in large flocks in central Australia (Masure & Allee 1934; Wyndham 1980; Farabaugh et al. 1998), are widely available from commercial suppliers and can be bred readily in captivity. Their repertoire of calls is acquired through vocal imitation (Farabaugh et al. 1994; Hile et al. 2000; Hile & Striedter 2001), and there is a substantial literature relating to budgerigar neurobiology (e.g. Jarvis & Mello 2000). However, as yet, there is no compelling evidence of motor imitation, or of nonimitative social learning, in budgerigars.

Budgerigars have not, to our knowledge, been tested for nonimitative social learning, and tests for motor imitation have produced predominantly negative results. Dawson & Foss (1965) reported demonstrator-consistent responding in budgerigars that had seen a conspecific removing a cover from a food cup using either its beak or its feet. However, several attempts to replicate this effect have failed (Galef et al. 1986; Moore 1992; R. Boakes, personal communication), and in the only reported successful replication, Galef et al. (1986) found the effect to be of brief duration and marginal significance.

The elusiveness and fragility of the Dawson & Foss effect may reflect lack of imitative ability on the part of budgerigars, but there are other explanations. For example, foot use and beak use may not be sufficiently discriminable for budgerigar observers, flat lids may elicit strong response tendencies that compete with the effects of conspecific observation, and/or procedures, like those of Dawson & Foss (1965) and Galef et al. (1986), in which observers are given one demonstration trial and one test trial daily, may not be optimal for detecting imitation.

To seek evidence of motor imitation and nonimitative social learning in budgerigars, we used a two-object/two-action test that has yielded positive results for both kinds of social learning in starlings (Campbell et al. 1999; Fawcett et al. 2002). In this test, observers see a conspecific demonstrator repeatedly removing one of two stoppers from the horizontal surface of a food box, either by pulling the stopper up or by pushing it down into the box, and after each daily demonstration session they are given access to both stoppers and rewarded with food for all removal responses in a fixed time period, regardless of which stopper is removed and the direction of its displacement. A significant bias in favour of responding to the same object/stopper as the demonstrator implies nonimitative social learning, that the observers were attracted to the object as a result of seeing a conspecific touch it, and a reliable bias in favour of using the same upward or downward extraction method as the demonstrator suggests that the observers have engaged in motor imitation.

Thus, we attempted to replicate in the budgerigar, the effects of imitative and nonimitative learning previously observed in starlings. We extended previous work using the two-action procedure by investigating sex differences in imitation, and examining the degree to which nonimitative social learning in the two-object/two-action test depends on colour rather than spatial cues. Reports that female budgerigars are more active than males, and that they dominate males in mixed flocks (e.g. Masure & Allee 1934), raise the possibility that males and females differ in the readiness with which they engage in imitation learning, and therefore that either males or females may be more appropriate for research investigating the mechanisms of imitation. Turning to nonimitative social learning, Campbell et al. (1999) found that starlings showed a bias in favour of responding to the same stopper as their demonstrator when the two coloured stoppers remained in the same locations during observation and testing, and across test trials. Consequently, this experiment did not establish whether observers encoded and preferred the colour of the object manipulated by their demonstrators, or whether they used a combination of colour and location cues. We sought to distinguish these possibilities by examining observers' object choice behaviour not only when the locations of the coloured stoppers were constant across test trials and the same as during observation, but also when they varied randomly across test trials and matched the observed configuration on only 50% of occasions.

METHODS

Subjects

We used 36 juvenile budgerigars. Eight of these were randomly assigned the role of demonstrator, and the remaining 28 were observers. They were obtained from a commercial supplier, and assigned to experimental groups, at approximately 8 weeks of age, before sex could be accurately determined. Postexperimental inspection of the birds' ceres indicated that 13 observers and five demonstrators were female. The birds were maintained in groups of 8–10 (observers and their respective demonstrators together) on a 12:12 h light:dark cycle (light onset 0700 hours) at 22–23°C in grill and sheet metal cages (2.39×0.47 m and 0.47 m high), containing four perches and lined with sandsheets and gravel. Water, mineral blocks and cuttlefish shells were continuously available. Prior to the experiment, millet seed, millet sticks and honey sticks were available ad libitum. During the experiment, the birds were weighed daily and maintained at no less than 90% of free-feeding body weight (mean 35–38 g) through the provision of 4–6 g of millet seed per bird after each daily experimental session.

Apparatus

The birds were trained and tested in the holding room in a metal grill cage (0.66×0.34 m and 44 m high) surrounded by a white cardboard occluding screen (Fig. 1). The floor of the cage was lined with sandsheets, and it was divided in half across its width by a 1-cm-gauge metal grill. One of these compartments was used for
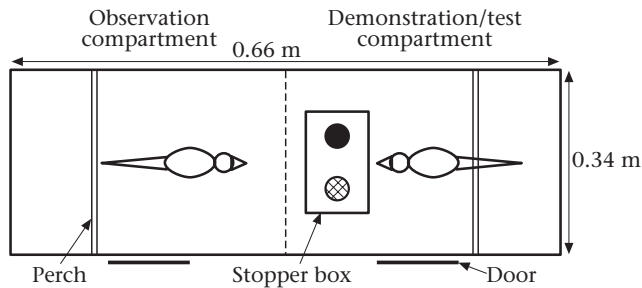
Figure 1. Plan of the apparatus.

demonstration and testing and the other housed the observer. Birds were placed in and removed from each compartment via separate doors on one of the two longest walls of the cage. Each compartment contained a plastic perch spanning its width and 0.23 m above the floor, 0.20 m from the dividing wall.

A white, rectangular aluminium box (0.21 × 0.1 m and 0.045 m high), with a white plastic lid, was placed on the floor of the demonstration/test compartment with its long axes adjacent to, and in the centre of, the dividing wall. This box stood on a rigid white plastic sheet (0.29 × 0.32 m), which was used to slide the box in and out of the test cage between trials, via a floor-level hatch in the wall of the demonstration compartment. The box was divided in half across its width by a sheet metal partition, so that either or both sections could be filled with millet seeds. Above each section, there was a hole (3.5 cm diameter) in the plastic lid providing access to the seeds beneath. The holes were 7 cm apart, 4 cm from the ends of the box, and 3.5 cm from the sides. The rim of each hole was lined with a thin (2-mm) strip of sponge and, at certain points in the experiment (specified below), blocked with a section of ping-pong ball 1.3 cm deep. Two strands of rigid metal wire (1 mm thick), arranged in a cross spanning the upper surface of this stopper, could be gripped by the birds. The upper concave surfaces of the two stoppers were coloured royal blue and black, respectively. These colours were chosen to contrast with the white lid of the food box, while being salient (cf. green), nonaversive (cf. red) and discriminable from one another. When demonstrators were using the apparatus, metal brackets were attached to either the upper or the lower rim of each stopper to prevent it from being pushed down into the box (upper brackets) or pulled up from the box (lower brackets).

The equipment was controlled, and the data were collected, manually by the experimenter (A.S.), who was positioned at all times ca. 0.6 m from the entrance side of the test cage. During demonstration and test trials, the occluding screen around the test cage ensured that the experimenter was not visible to the birds. All demonstration and test sessions were recorded with a Sony camcorder (AC-V25A) mounted 60 cm above the test cage.

Procedure

Prior to the experiment, we randomly assigned observer birds in equal numbers to one of four direction/colour

groups: up blue, down blue, up black and down black. Observers in the up groups saw the demonstrator pulling the stopper upwards, and those in the down groups saw the demonstrator pushing the stopper downwards into the box. In the blue groups the demonstrator removed the blue stopper, and in the black groups it removed the black stopper. We conducted the experiment in two replications. In the first replication, which consisted of 12 observers (three in each of groups up blue, down blue, up black and down black), the positions of the blue and black stoppers remained constant across all trials, whereas in the second replication, involving 16 observers (four in each direction/colour group), the positions of the blue and black stoppers varied randomly across demonstration trials and, independently, across observer test trials. The purpose of this manipulation was to investigate whether budgerigars can use not only a combination of colour and spatial cues to identify the object manipulated by their demonstrator (constant group), but also colour cues alone (variable group).

Each session began when the food box was placed in the test cage, and ended 15 min later when it was removed.

Demonstrator training

During initial daily sessions of demonstrator training, each bird was given exclusive access to the food box in the home cage. The stoppers were absent on these occasions, and both sections of the box were filled with millet seed. Once a bird had learned to feed from the box under these conditions, daily sessions were conducted in the demonstration compartment of the test cage, with the stoppers placed on the lid of the food box at some distance from the holes. Over sessions, the stoppers were moved closer to the holes until they were partially occluding, and then completely blocking, access to the seed. After an average of six sessions of this kind, each demonstrator removed the stopper and ate from the box at some point in the 15-min session. In subsequent sessions, the brackets were attached to the stoppers to prevent all but one of the four removal responses (black up, black down, blue up or blue down), depending on the demonstrator's group assignment, and, after each stopper removal, the birds were allowed to feed for a fixed period before the box was removed from the test cage and the stopper replaced for the next trial. The postremoval feeding period was gradually reduced from 60 to 15 s, and training was terminated when the birds reached a criterion of 10 successful responses in each of three successive test sessions. Another demonstrator, with the same group assignment as the training bird, was placed in the observation compartment during the last few sessions to promote habituation to the presence of another bird in the test cage.

Demonstrators and observer birds used similar response topographies when removing a stopper. While standing on the lid of the box, the bird moved its head towards the stopper. For an up response, the mandibles were then closed on the cross wire, and the head was pulled sharply upwards. 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, occasionally, on the floor of the test box. For down responses, a sharp downward thrust of the head brought the end of the beak into contact with a cross wire or the upper surface of the stopper, causing it to fall downwards on to the floor of the box.

Observer training and testing

Prior to demonstrator observation, the observers were habituated to the test apparatus and procedure, and trained to feed through the holes in the lid of the food box, during twice daily 'magazine training' sessions in the test cage. The stoppers were absent during these sessions. In the first, the birds were allowed to feed from the box for an unlimited period. In the second magazine training session, the experimenter terminated each feeding bout after 60 s by sliding the box out of the test cage, and initiated a new trial immediately by returning the box to its standard location in the cage. In subsequent sessions, the feeding period was gradually reduced to 15 s. Magazine training continued until the observers reached a criterion of 10 feeding bouts per session in three consecutive sessions, or after 14 sessions. During the final sessions of magazine training, the demonstrator assigned to each observer was present in the observation compartment while the observer fed from the food box.

Observers received 10 demonstration sessions, two each day for 5 successive days, and were tested after each of sessions 4–10, that is, seven times. At the beginning of each demonstration session, the observer was placed in the observation compartment for 2 min to habituate to its surroundings, and then the demonstrator was placed in the demonstration compartment. After ca. 1 min, the food box was inserted into the test cage and the demonstrator was allowed to begin responding. The demonstration session ended when the demonstrator had removed a stopper and eaten from the box for 15 s on 10 occasions, or when 15 min had elapsed. Between stopper removal responses, the experimenter slid the box out of the cage, replaced the stoppers, and returned the box to the cage. At the end of the session, the food box and demonstrator were removed from the test cage.

There was an interval of ca. 2 min between demonstration and test sessions. During this time, the observer remained in the observation compartment while the experimenter replaced the sandsheet lining of the demonstration/test compartment, wiped the lid of the food box with a damp cloth to remove any deposits, and replaced the stoppers used by the demonstrator with a pair used exclusively for observer testing. The food box was then replaced in the demonstration/test compartment, and the grill dividing the two compartments was lifted to allow the observer to move into that area from the observation compartment. When the observer had been ushered between compartments, the grill was lowered. In the ensuing 15 min, the observers were free to remove either stopper in either direction, and were rewarded with 15 s of access to food for responses of any of these four types. Between trials, the box was removed from the test cage and the stopper replaced in the same

way as during demonstration sessions. At the end of Test 3, and after each subsequent test, birds that had not yet removed a stopper and fed from the box at any time during testing were given an additional magazine training session to remind them that food was available in the box and thereby to sustain task motivation. The stoppers were absent during these sessions, and therefore this experience could not influence the colour or direction of subsequent removal responses.

Training and testing occurred between 0900 and 1700 hours each day. The order in which observers were run each day was randomized across groups to control for time of day.

Data scoring

Videotapes of the observers' test sessions were scored by two independent raters, one of whom was blind to the viewed animal's group assignment. Whenever an observer removed a stopper, the raters recorded the direction of movement (up or down) and the colour (blue or black) of the stopper. In addition, the raters recorded the frequency of approaches to each of the two stoppers. An approach was scored whenever the overhead camera angle indicated that the beak of a bird that was standing on the box had entered the area immediately above one of the two stoppers, that is when the tip of the beak broke the perimeter line of the stopper. The raters were in agreement regarding the colour and direction of stopper removal, and the colour of object approaches, in 100% of a randomly selected 25% of test sessions.

Three measures of test performance were calculated for each bird. (1) A directional discrimination ratio, calculated by dividing the number of up removal responses by the total number of removal responses, was used to assess whether observers tended to remove the stopper in the same direction as their demonstrator. We expected observers of up responding to have higher directional discrimination ratios than observers of down responding. (2) We used a removal colour discrimination ratio, calculated by dividing the number of removals of the blue stopper by the total number of removal responses, and (3) an approach colour discrimination ratio (number of approaches to the blue stopper divided by the total number of approaches), to investigate whether observers were biased in favour of removing the stopper of the same colour as their demonstrator. In this case, we expected observers of blue stopper removal to have higher colour discrimination ratios than observers of black stopper removal. Up responses and blue responses were chosen arbitrarily as the numerators in these calculations; had down and black responses been selected instead, the resulting ratios would be complementary and the statistical results identical.

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 allowed us to examine how, if at all, effects of conspecific observation changed as observers gained experience of direct interaction with
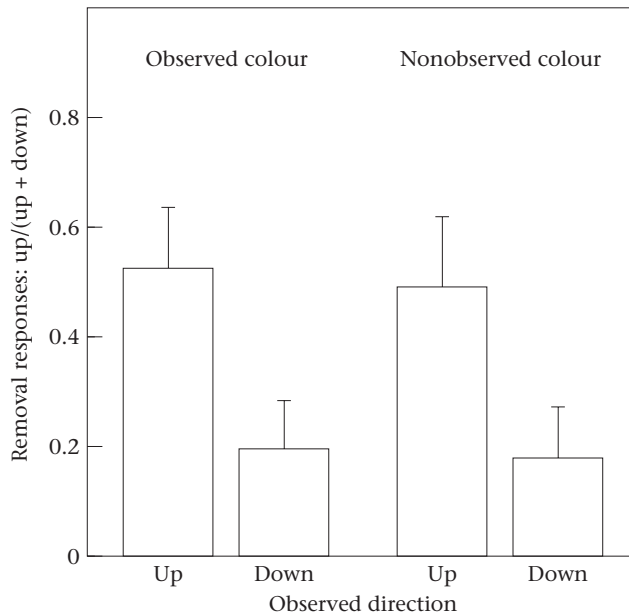
Figure 2. Removal direction discrimination ratios ($\bar{X} \pm$SE) calculated across all test sessions for responses made to the stopper removed by the demonstrator (observed colour) and to the alternative stopper (nonobserved colour), by birds that observed up or down responding.

the apparatus, that is with increasing opportunity for individual learning.

RESULTS

Of the 28 observers tested, three failed to remove a stopper during any of the test sessions, and were therefore excluded from the analysis. All three of the excluded birds were tested in the constant group, one from each of groups down blue, up black and down black. Thus, the sample sizes were: up blue=7, up black=6, down blue=6, down black=6. The median number of test sessions in which observers made approach responses was seven, and the median number in which they made removal responses was five. Only six birds made removal responses in all seven sessions. On average ± SE, observer birds removed a stopper 58.2 ± 12.6 times in the course of the seven test sessions, 5.64 ± 1.4 times during the first test in which they made a removal response, and were given 1.76 ± 0.33 additional magazine training sessions. The frequency of removal responses and of additional magazine training sessions did not vary with group assignment ($F_{1,21}$ <1 in all cases).
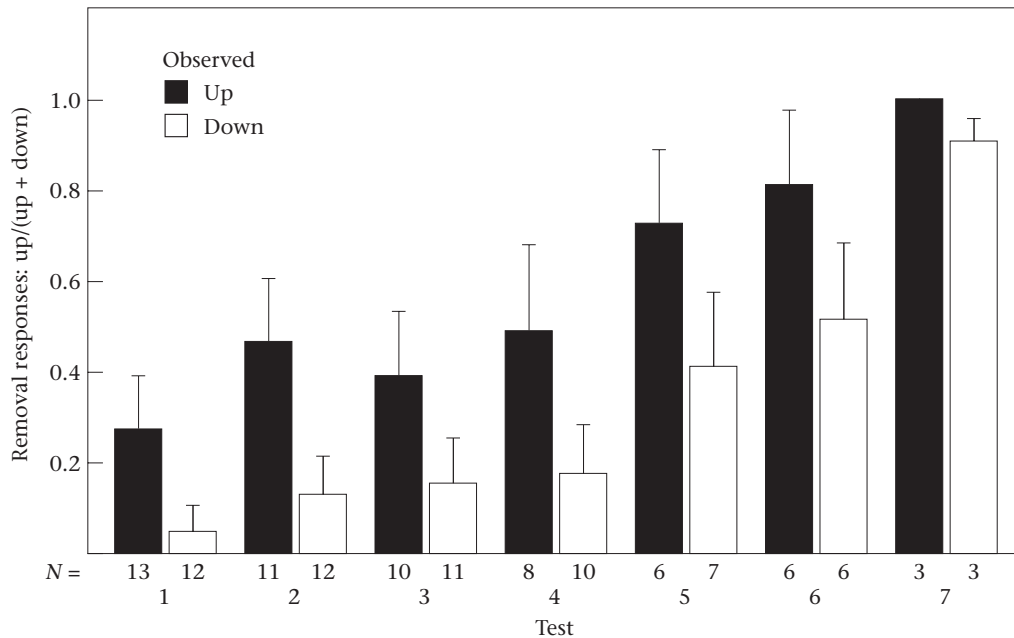
Direction Discrimination

Figure 2 gives mean directional discrimination ratios, calculated across all test sessions, for birds that observed up and down responding, when they were removing the stopper of the same colour as their demonstrator (observed colour) and when they were removing the other stopper (nonobserved colour). In spite of an overall bias in favour of pushing the stopper downwards,

observers of up responding made a greater proportion of up removal responses than observers of down responding, when removing both objects. Directional discrimination ratios based on all removal responses, regardless of the test session in which they occurred, were subjected to a mixed-model ANOVA in which direction (up versus down) and location (constant versus variable) were the between-subjects factors, and measure (observed colour versus nonobserved colour) was the within-subjects factor. Two birds (one in group up blue, and the other in group up black) never removed the stopper of the nonobserved colour, and therefore could not be included in this analysis. In spite of this loss of power, the analysis indicated a main effect of direction ($F_{1,19}$=7.01, P=0.016), and no effects or interactions involving location ($F_{1,19}$<1) or measure ($F_{1,19}$ =1.12, NS).

To determine whether the observers' bias in favour of removing stoppers in the same direction as their demonstrators varied during testing, we calculated a directional discrimination ratio for each test session (Fig. 3). Too few birds contributed data to Tests 6 and 7 to allow the data in Fig. 3 to be subjected to factorial analysis involving both direction and location variables. The mixed-model ANOVA examining performance on successive tests as a function of direction showed that the proportion of up responses increased across tests in a linear fashion ($F_{1,4}$=11.00, P=0.03), but that this effect did not vary or interact with observed direction ($F_{1,4}$<1 in both cases). The absence of an effect of observed direction in this analysis is likely to have been due to its limited power; as indicated in Fig. 3, only six birds made removal responses in all seven test sessions. Separate analyses of the Test 1, Test 2 and Test 3 ratios showed that observers of up responding made a greater proportion of up responses than observers of down responding (one-tailed tests; Test 1: $F_{1,21}$=6.25, P=0.02; Test 2: $F_{1,19}$=6.09, P=0.02; Test 3: $F_{1,17}$=3.68, P=0.036), with no reliable effects of location ($F_{1,21}$<1, $F_{1,19}$<1, $F_{1,17}$<1 , respectively) or direction × location interactions (Test 1: $F_{1,21}$=1.49; Test 2: $F_{1,19}$=2.20; Test 3: $F_{1,17}$=2.41, all NS). Thus, although detection of enduring effects of conspecific observation was opposed by an overall tendency for increasing experience with the stopper box to result in more up responding, the directional matching effect persisted throughout at least three 15-min test sessions in which an average ± SE of 24.1 ± 4.9 removal responses were made.

For many observer birds, the first removal response seemed to be accidental in that it was not followed by exploration or consumption of the food beneath the stopper. Counting only those removals that were followed by feeding, 11 observers made their first response in the same direction as their demonstrator while four made their first response in the opposite direction (χ_1^2=3.27, P=0.035, one-tailed). Thus, the directional matching effect was early as well as persistent; it was detectable on the first occasion when the observer birds removed the stopper and fed from the box.

Averaging across test sessions, female observers made more removal responses than males ($\bar{X} \pm$ SE; female: 83.6 ± 22.4, N=11; male: 38.1 ± 12.1, N=14; $F_{1,17}$=4.79, P=0.04), and a higher proportion of up responses, but the

Figure 3. Removal direction discrimination ratios ($\bar{X}\pm$SE) for Tests 1–7 and birds that observed up or down responding. *N* values are given at the base of each bar.
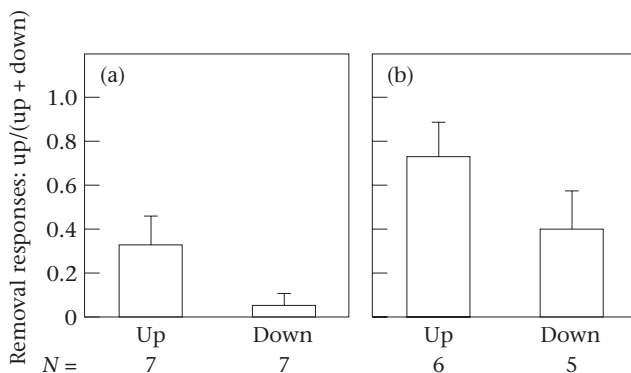
Figure 4. Removal direction discrimination ratios ($\bar{X}\pm$SE) calculated across all test sessions for (a) male and (b) female observers of up and down responding.

demonstrator-consistent directional bias was equally strong in males and females. A three-way ANOVA (direction × sex × location) applied to the data shown in Fig. 4 indicated a main effect of direction ($F_{1,17}=6.51$, $P=0.021$) and a main effect of sex ($F_{1,17}=7.09$, $P=0.016$), but no other effects or interactions were significant ($F_{1,17}<1$ in all cases).

Object Discrimination

Analysis of removal responses failed to provide any evidence that observers in either the constant or the variable group were influenced in their choice of stopper to be manipulated by the colour of the stopper removed by their demonstrator. The mean removal colour discrimination ratio for blue observers was numerically greater than that of black observers in both the constant

and the variable groups ($\bar{X}\pm$SE; constant: blue: 0.69 ± 0.16; black: 0.56 ± 0.13; variable: blue: 0.55 ± 0.06; black: 0.44 ± 0.07), but an ANOVA failed to show main effects of colour ($F_{1,21}=1.40$) or location ($F_{1,21}=1.77$), or a significant interaction ($F_{1,21}<1$).

Informal observation of the observer birds during testing suggested that the majority of their approach responses were made at the beginning of each test session, and preliminary statistical analysis confirmed this impression. It showed that birds in the variable group made more approaches to the stoppers than those in the constant group ($F_{1,21}=6.13$, $P=0.022$), and that in both groups approaches were more frequent in the first 5 min of each test session than during the remaining 10-min period ($F_{1,21}=22.43$, $P<0.0001$) (Fig. 5). The former effect, which suggests that movement of the stoppers between trials promoted their exploration by observers, does not jeopardize the validity of approach ratio analysis because birds that had observed blue and black stopper removal did not differ in the frequency of their approach responses ($F_{1,21}<1$), and the colour and location variables did not interact ($F_{1,21}=1.07$, NS). However, the fact that observers made many more approach responses at the beginning of test sessions than subsequently suggested that approach colour discrimination ratios for the first 5 and the latter 10 min of testing should be analysed separately.

Analysis of the approach colour discrimination ratios for the last 10 min of each test session, when the frequency of approaches was relatively low, revealed no differences between observers of blue and black stopper removal, in either the constant or the variable group. Figure 6 shows approach colour discrimination ratios for the first 5 min of each test session. Data from the 17 birds that made approach responses in the first 5 min of all seven test sessions were subjected to a mixed-model
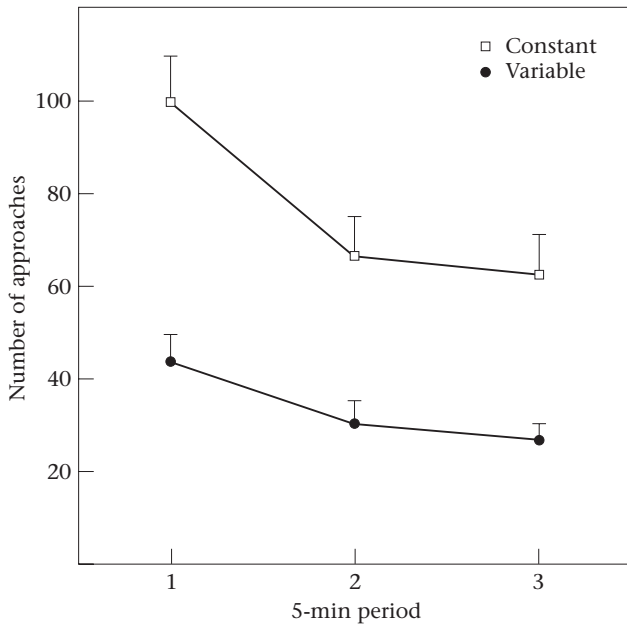
Figure 5. Number of approaches to the stoppers ($\bar{X}\pm$SE) calculated across test sessions for observer birds in the constant and variable groups. In the former group the positions of the blue and black stoppers were constant across trials and in the latter they varied. Approaches in the three successive 5-min periods comprising test sessions are shown separately.

ANOVA in which observed colour (blue versus black), location (constant versus variable) and test session (1–7) were factors. This revealed a main effect of colour, with observers of blue stopper removal making a higher proportion of blue responses ($F_{1,13}$=7.63, P=0.016), and significant interactions between colour and location ($F_{1,13}$=13.60, P=0.003), and between colour and test

($F_{6,78}$=4.13, P=0.001). Simple effects analysis exploring the former interaction showed that the difference between observers of blue stopper removal and black stopper removal was significant in the constant group ($F_{1,13}$=13.63, P=0.003) but not in the variable group ($F_{1,13}$<1).

DISCUSSION

The budgerigar would be an ideal species for research on avian motor imitation because it is hardy and accessible, a vocal mimic, and there is a substantial literature on its neurobiology. In contrast with previous experiments, which have tried and failed to find robust evidence of motor imitation in the budgerigar (e.g. Galef et al. 1986; Moore 1992), our results suggest that this species also fulfils the central requirement for an avian model of motor imitation, of reliably copying body movements. This is implied by the reported effects of conspecific observation on directionality of responding. Birds that saw a demonstrator removing a stopper with an upward or a downward motion were biased in favour of using the same movement, not only when they detached the stopper and fed from the box for the first time, but throughout at least three 15-min test sessions encompassing an average of 24 removal responses per bird. This contrasts with the finding of Galef et al. (1986) that budgerigars use the same method as their demonstrators only on the first two or three occasions when they remove a flat cover from a food cup.

The detection of a directional matching effect on the birds' first responses is striking given the modest size of our sample, and the vulnerability of single response measures to sources of random variation. However, the effect detected over subsequent test sessions provides equally compelling evidence that the birds were
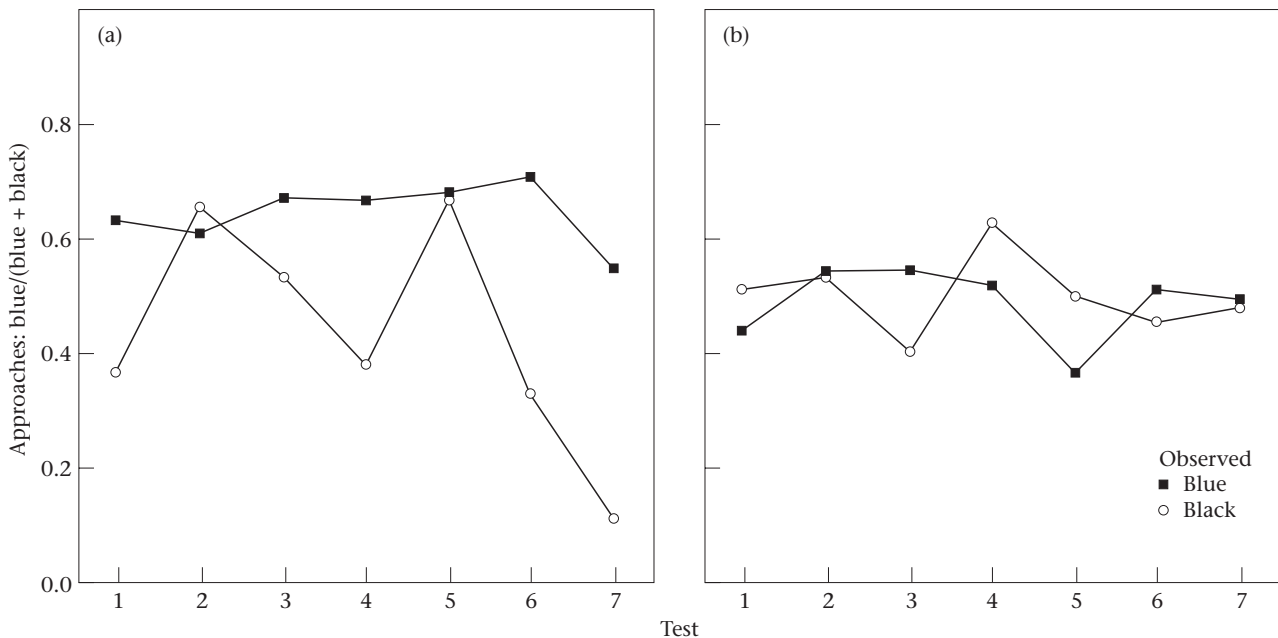
Figure 6. Mean approach colour discrimination ratios for Tests 1–7 and birds that observed blue or black stopper removal. (a) Constant; (b) variable groups.

matching their demonstrators' response direction because observation experience is its only potential source. If the birds had been selectively rewarded on test for responding in the same direction as their demonstrators, their matching tendency could have been due to individual learning alone, but they were rewarded with access to food for all removal responses.

The birds' tendency to remove stoppers in the same direction as their demonstrators could not be due to social facilitation because observers of up and down responding were exposed equally to the presence and activity of a conspecific prior to testing. The effect is unlikely to be due solely to stimulus enhancement or observational conditioning because demonstrators of up and down responding both displaced the objects, and fed from the box below, in a way that was likely to draw attention to the stoppers (stimulus enhancement), and which provided observers with the opportunity to learn a stopper–food contingency (observational conditioning). Similarly, local enhancement, in which an observer is attracted to deposits left on the manipulandum by the demonstrator, is an implausible explanation. It is not clear what kind of deposits could have been made by demonstrator birds that would have survived intertrial cleaning.

The only plausible alternative to motor imitation is emulation learning. It is possible that, instead of learning to remove stoppers with an up or down thrust of the head and mandibles (imitation), the birds learned by observation that an upward or downward trajectory of the stopper predicted the sight of food or a feeding conspecific (emulation). This is unlikely given that upward removal of the stopper, by both demonstrators and observers, sometimes resulted in the stopper landing inside the box, but it cannot be ruled out. The results of most two-action tests in birds and primates could, similarly, be due to imitation or emulation (e.g. Whiten 1998; Custance et al. 1999; Voekl & Huber 2000; Huber et al. 2001; Stoinski et al. 2001). Research showing that pigeons and Japanese quail tend to depress a treadle using the same pecking or stepping movements as their demonstrator (e.g. Dorrance & Zentall 2001) is exceptional in this respect. These results could not be due to emulation learning because the treadle manipulandum moves through the same trajectory when operated by pecking and stepping. However, they are subject to another interpretative problem: birds that are housed and fed in groups are likely to form a Pavlovian association between the sight of a pecking conspecific and the availability of food, leading them to make exploratory and consummatory responses appropriate to food (i.e. to peck) whenever they see another bird pecking. Observation of a demonstrator pecking a novel object (e.g. a treadle) provides the opportunity for second-order conditioning in which the object also becomes a signal for the availability of food (Rescorla 1980). Thus, a tendency to peck an object more after observing pecking than after observing stepping could be due, not to copying of body movements, but to a variety of nonimitative social learning in which the manipulandum acquires excitatory properties through second-order conditioning.

The pecking/stepping effect would be less vulnerable to this interpretative problem if it had been shown conclusively, not only that observation of pecking promotes pecking, but also that observation of stepping promotes stepping (Heyes & Ray 2000). This could be achieved by comparing the behaviour of each group to that of non-exposed control birds who observed a demonstrator feeding from the apparatus, but not operating on the manipulandum, prior to testing. The addition of a similar group to the design of the present experiment would establish whether budgerigars copy upward responding, downward responding or both. However, given that both response types involved pecking movements, the effects we report could not be due to second-order conditioning of the kind outlined above, and therefore it is not clear what theoretical purpose would be served by resolution of this issue.

The present study investigated for the first time whether male and female birds differ in the readiness with which they will copy a conspecific. In their classic study of the social ecology of the budgerigar, Masure & Allee (1934) reported that nonbreeding females dominate males in mixed flocks, and, more generally, that 'the mature female [budgerigar] is more noisy and less tractable than is the mature male'. The juvenile females in our present study were more 'noisy' than the males in that they made more removal responses, but they were no less 'tractable'; the effects of conspecific observation on directionality of responding were equally strong in male and female birds. In view of the dominance of nonbreeding females, it would be interesting to compare the effects on males and females of observing either male or female demonstrators. Factorial analysis of this kind was not possible in our study because, at the time of group assignment, the birds were too young for reliable determination of gender.

A subsidiary aim of the present study was to test for nonimitative social learning in the budgerigar by investigating whether observers would respond more to the coloured stopper manipulated by their demonstrator than to the alternative stopper. An effect of this kind was not detected when we analysed observers' removal responses, but, during the first 5 min of each test session, when they were investigating the stoppers most intensively, observers in the constant group preferentially approached the demonstrator's stopper. This result suggests that observation of a demonstrator's activity drew the observer's attention to the object (stimulus enhancement), or facilitated learning of an association between the object and food (observational conditioning). The occurrence of this effect in the constant group, when the blue and black stoppers remained in the same locations over trials, but not in the variable group, when the locations of the coloured stoppers varied over trials, suggests that the observer birds did not use colour cues alone to identify the object manipulated by their demonstrators. This is unlikely to have been due to an incapacity to discriminate the colours, because they were of different brightness. In the constant group, the birds may have used spatial cues alone or a combination of spatial and colour cues. In the former case, but not in the latter, one

would expect the effect to persist when the two objects are of the same colour.

In the constant group, preferential approach to the demonstrator's object was detected in the first 5 min of each test, but not in the later 10-min test period. Combined with the fact that the bias detectable in the first 5 min did not decline significantly across test sessions, this implies that the effect of demonstrator observation on approach behaviour weakened in the course of each test period, possibly overlaid by the effects of individual learning, but was re-established in each subsequent demonstration session.

When tested using a similar two-object/two-action procedure, starlings showed, not only preferential approach, but a bias in favour of removing the same stopper as their demonstrator (Campbell et al. 1999). The absence of an effect of observed object on removal responses in our study suggests either that nonimitative social learning has a weaker effect on budgerigars' performance in this procedure, or that, as currently implemented, the procedure is less sensitive to this kind of learning in budgerigars than in starlings. For example, it is possible that exploratory movements of the kind scored as 'approaches' are more vigorous in starlings, and therefore more likely to result in stopper displacement.

In conclusion, our findings are consistent with the hypothesis that budgerigars are capable of learning by imitation. The stopper two-action test used in the present experiment yielded early and durable matching effects in both male and female birds, and therefore provides a promising basis for analytical investigation of avian motor imitation.

Acknowledgments

References

Akins, C. K. & Zentall, T. R. 1996. Imitative learning in male Japanese quail using the two-action method. *Journal of Comparative Psychology*, **110**, 316–320.

Akins, C. K. & Zentall, T. R. 1998. Imitation in Japanese quail: the role of demonstrator reinforcement. *Psychonomic Bulletin and Review*, **5**, 694–697.

Akins, C. K., Klein, E. D. & Zentall, T. R. In press. Imitative learning in Japanese quail using the bi-directional control procedure. *Animal Learning and Behavior*.

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.

Custance, D., Whiten, A. & Fredman, T. 1999. Social learning of an artificial fruit task in capuchin monkeys. *Journal of Comparative Psychology*, **113**, 13–23.

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

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

Farabaugh, S. M., Linzenbold, A. & Dooling, R. J. 1994. Vocal plasticity in budgerigars: Evidence for social factors in the learning of contact calls. *Journal of Comparative Psychology*, **108**, 81–92.

Farabaugh, S. M., Dent, M. L. & Dooling, R. J. 1998. Hearing and vocalizations of wild-caught Australian budgerigars. *Journal of Comparative Psychology*, **112**, 74–81.

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.

Fritz, J. & Kotrschal, K. 1999. Social learning in common ravens. *Animal Behaviour*, **57**, 785–793.

Galef, B. G., Jr. 1988. Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef eds.) Hillsdale, New Jersey: L. 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.

Heyes, C. M. 1994. Social learning in animals: categories and mechanisms. *Biological Reviews*, **69**, 207–231.

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

Heyes, C. M. & Ray, E. D. 2000. What is the significance of imitation in animals? *Advances in the Study of Behavior*, **29**, 215–245.

Hile, A. G. & Striedter, G. F. 2001. Call convergence within groups of female budgerigars. *Ethology*, **106**, 1105–1114.

Hile, A. G., Plummer, T. K. & Striedter, G. F. 2000. Male vocal imitation produces call convergence during pair bonding in budgerigars. *Animal Behaviour*, **59**, 1209–1218.

Huber, L., Rechberger, S. & Taborsky, M. 2001. Social learning affects object exploration and manipulation in keas. *Animal Behaviour*, **62**, 945–954.

Jarvis, E. D. & Mello, C. V. 2000. Molecular mapping of brain areas involved in parrot vocal communication. *Journal of Comparative Neurology*, **419**, 1–31.

Kaiser, D. H., Zentall, T. R. & Galef, B. G. 1997. Can imitation in pigeons be explained by local enhancement together with trial-and-error learning? *Psychological Science*, **8**, 459–460.

Lefebvre, L., Templeton, J., Brown, K. & Koelle, M. 1997. Carib grackles imitate conspecific and zenaida dove tutors. *Behaviour*, **134**, 1003–1017.

Masure, R. H. & Allee, W. C. 1934. Flock organization of the shell parakeet *Melopsittacus undulatus* Shaw. *Ecology*, **15**, 388–397.

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.

Rescorla, R. A. 1980. *Pavlovian Second-order Conditioning*. Hillsdale, New Jersey: L. Erlbaum.

Stoinski, T. S., Wrate, J. L., Ure, N. & Whiten, A. 2001. Imitative learning by captive western lowland gorillas in a simulated food-processing task. *Journal of Comparative Psychology,* **115**, 272–281.

Thorndike, E. L. 1898. Animal intelligence. *Psychological Review Monographs*, **2**, No. 8.

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. *Journal of Comparative Psychology*, **112**, 270–281.

Wyndham, E. 1980. Diurnal cycle, behaviour and social organization of the budgerigar. *Emu*, **80**, 25–33.

Zentall, T. R., Sutton, J. E. & Sherburne, L. M. 1996. True imitative learning in pigeons. *Psychological Science*, **7**, 343–346.