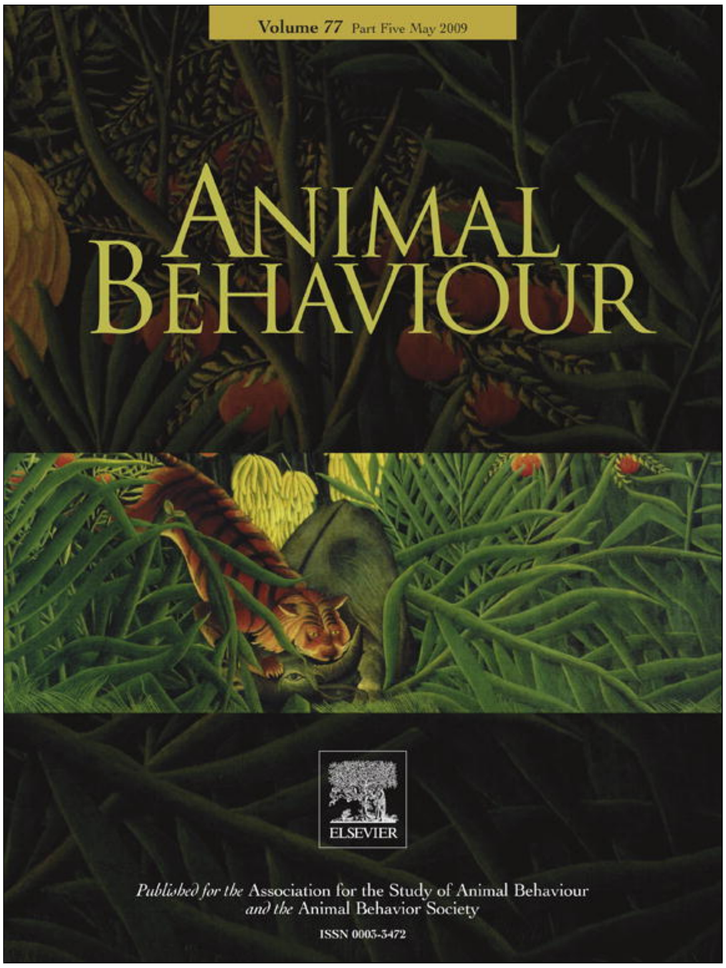
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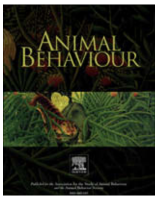

Imitative pecking by budgerigars, *Melopsittacus undulatus*, over a 24 h delay

Charlotte Richards [a,1], Kieron Mottley [b,2], John Pearce [b,2], Cecilia Heyes [a,c,*]

[a] *Department of Psychology, University College London*
[b] *School of Psychology, Cardiff University*
[c] *All Souls College, University of Oxford*

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On video, budgerigars observed a conspecific demonstrator depressing a stopper by pecking or by stepping and then feeding from the box below. The observers were given access to the stopper, immediately after observation or following a 24 h delay, and we recorded the proportion of their stopper removal responses that were made by pecking and by stepping. In experiments 1a and 1b, observers of pecking made a greater proportion of pecking responses than observers of stepping, and this effect did not vary between the immediate and delayed test groups. The results of experiment 2 replicated this effect with a delayed test, and suggested that it was due to imitation of pecking. Control birds that observed a demonstrator feeding, but did not see stopper removal, made a smaller proportion of pecking responses than pecking observers, but their behaviour did not differ from that of stepping observers. These findings are consistent with the associative sequence learning model of imitation, which suggests that the capacity to imitate a particular action depends on correlated experience of observing and executing that action.

It has been well established using two-action tests in the laboratory that a variety of bird species show a pecking–stepping imitation effect. When one group of birds has observed a conspecific demonstrator pecking an object, and a second group has observed a demonstrator stepping on the object, the members of both groups typically direct both pecks and steps to the object. However, the proportion of pecking to stepping responses is biased towards pecking in the birds that observed pecking, and towards stepping in the birds that observed stepping (e.g. budgerigars: Dawson & Foss 1965; pigeons, *Columba livia*: Zentall et al. 1996; Nguyen et al. 2005; Saggerson et al. 2005; quail, *Coturnix japonica*: Akins & Zentall 1996; Dorrance & Zentall 2001).

The term ‘pecking–stepping imitation effect’ describes this result but does not give it a psychological explanation. The principal challenge is to explain how the birds manage to overcome the ‘correspondence problem’ (Brass & Heyes 2005), that is, how to translate visual input from the demonstrator’s behaviour (e.g. the sight of another bird pecking) into motor output (e.g. pecking behaviour by the observer) that looks the same from a third-party perspective. This is difficult to explain because pecking yields different visual inputs when it is observed and executed; ‘you pecking’ and ‘me pecking’ do not look the same from the focal bird’s perspective. When an observer watches another bird pecking, it sees rapid movement of a beak, head and neck, but when the observer engages in pecking behaviour, it sees the object that it is pecking and/or surrounding objects; it cannot see its own head and neck.

A number of authors have suggested that, in humans, the correspondence problem is solved by a complex cognitive mechanism that represents actions in a ‘symbolic’ (Bandura 1969; see also Piaget 1962) or ‘supramodal’ (Meltzoff & Moore 1997) code, in a way that is neither sensory nor motor, and is therefore perspective independent. However, these theories do not explain in any detail the nature or origins of these cognitive mechanisms, and simpler accounts of how humans solve the correspondence problem are gaining empirical support in cognitive psychology and cognitive neuroscience (e.g. Catmur et al. 2007, 2008; reviewed in Brass & Heyes 2005).

One of these simpler accounts, the associative sequence learning (ASL) model (Heyes & Ray 2000), offers a potential explanation for

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[*] Correspondence: C. Heyes, All Souls College, Oxford OX1 4AL, U.K.
E-mail address: cecilia.heyes@all-souls.ox.ac.uk (C. Heyes).

[1] C. Richards is at the Department of Psychology, University College London, Gower Street, London WCIE 6BT, U.K.

[2] K. Mottley and J. Pearce are at the School of Psychology, Cardiff University, Cardiff CF10 3AT, U.K.

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the pecking–stepping imitation effect in birds. It suggests that the sight of another bird engaging in a behaviour, B, will activate a motor representation of B in the observer, a necessary condition for the performance of B, to the extent that the observer has prior experience of seeing and doing B together. More specifically, and using pecking as an example, the sight of pecking will elicit a motor representation of pecking, and overt pecking behaviour, to the extent that the observer bird has had 'correlated experience' of observing and executing pecking behaviour, experience in which the sight of pecking and the performance of pecking occur in close temporal proximity and a contingent (or predictive) relationship with one another. (Note that this kind of learning does not depend on reward or other varieties of 'reinforcement'.) This kind of experience is available in social-foraging situations where birds peck to obtain food while accompanied by other birds doing the same. Thus, the ASL model suggests that the pecking–stepping imitation effect is mediated by basic processes of associative learning.

We tested the ASL model by addressing two questions about the pecking–stepping imitation effect. (1) Does the effect endure when there is a 24 h interval between observation and testing? (2) Does the effect arise from imitation of pecking, imitation of stepping or both? We addressed the second question by adding a control group to the conventional pair of groups, one that observes pecking and another that observes stepping. The control birds observed an active conspecific, but did not see their demonstrator stepping or pecking the target object.

The ASL model predicts that the effect will endure over a 24 h delay because it assumes that imitation, itself a product of associative learning, will give rise to further associative learning. More specifically, it assumes, for example, that imitative pecking in a distinctive context (the test cage) will become conditioned to that context. Consequently, when the observer bird is reintroduced to the test cage after a delay, the contextual cues will elicit pecking. Experiments with pigeons, showing that observation of pecking and stepping can facilitate reversal of a conditional discrimination (Dorrance & Zentall 2002; Saggerson et al. 2005), have provided evidence that a basic imitative tendency can support this kind of stimulus (context)–response (pecking) learning.

With respect to the second question, the ASL account suggests that birds that feed in social groups will show a robust tendency to imitate pecking, and that the effect may be weaker or absent for stepping. This is because social foraging provides many opportunities for a bird to peck while observing other birds pecking, and thereby to experience a contingency, or predictive relationship, between observation and execution of pecking. It is not clear, however, that there are circumstances that reliably provoke birds to step while observing others stepping. In principle, the contingency experience that the ASL model says is necessary for imitation of stepping could be obtained through self-observation: by a bird looking at its own feet while stepping. However, self-observation of stepping would need to occur systematically and often in order to prevent the contingency from being eroded by other experiences, in which stepping is on some occasions observed but not performed, and on other occasions performed but not observed. We know of no evidence of the occurrence of this kind of systematic self-observation.

Rather than live demonstrators, we used video images of conspecific action to address these questions about the durability and symmetry of the pecking–stepping imitation effect in birds. A previous study showed that, when budgerigars observe thin-film transistor images of a conspecific removing a stopper from a food box by pulling it upwards or by pushing it downwards, they tend to adopt the upwards or downwards technique observed (Mottley & Heyes 2003). This suggests that budgerigars will copy the behaviour of 'virtual demonstrators', but it does not show unambiguously that they imitate body movements rather than object movements presented in video format. In principle, the birds in the Mottley & Heyes (2003) study could have been reproducing the observed effect of the demonstrator's action on the stopper (upward or downward movement), rather than the actions used to bring about this effect (pulling or pushing). The former effect has been described as 'emulation' (Tomasello 1996). Consequently, before examining the durability (experiments 1b and 2) and symmetry (experiment 2) of the pecking–stepping imitation effect, we completed a preliminary experiment (1a) to check that the basic effect can be obtained with video stimuli.

EXPERIMENTS 1a AND 1b

Experiments 1a and 1b each included two groups of budgerigars: one that observed a demonstrator pecking a stopper (Group Peck), and another that observed a demonstrator stepping on the stopper (Group Step), to gain access to food in the box below. In both experiments, the birds underwent the same preliminary training, they observed their demonstrators' behaviour on video, and the demonstrators' pecking or stepping behaviour displaced the stopper downwards into the food box. In the first experiment the observers were tested, by being given access to the stopper, immediately after each observation trial, whereas in the second experiment there was an interval of 24 h between observation and testing.

If the pecking–stepping imitation effect, previously found with live demonstrators (e.g. Dawson & Foss 1965; Akins & Zentall 1996; Zentall et al. 1996; Dorrance & Zentall 2001; Nguyen et al. 2005; Saggerson et al. 2005), can also be generated by video images of demonstrator behaviour, then one would expect the results of experiment 1a to provide evidence of demonstrator-consistent behaviour. That is, relative to observers of stepping, observers of pecking should make proportionally more pecking than stepping responses on test. If the pecking–stepping imitation effect endures across a 24 h delay between observation and testing, demonstrator-consistent behaviour should also be observed in experiment 1b. If the effect is weaker when testing is delayed rather than immediate, the difference between Group Peck and Group Step should be smaller in experiment 1b than in experiment 1a.

Methods

Subjects

The observers were 38 juvenile budgerigars, of mixed sex (24 in experiment 1a and 14 in experiment 1b), obtained from a commercial supplier. In each experiment, the birds were randomly assigned in equal numbers to observe a video of a conspecific demonstrator pecking at (Group Peck) or stepping on (Group Step) a stopper, displacing it downwards, and feeding from the box below.

All birds were allowed to habituate to the laboratory for at least 1 week before the experiments began. They were housed in groups in large breeding cages (100 × 50 cm and 50 cm high), with free access to water, grit and cuttlefish. Prior to the experiment, and during the initial magazine training, they were fed ad libitum on millet. During the second half of training and the entire test phase, they were fed 3–6 g of millet/bird per day after the completion of training/testing and were weighed daily. Their weight was not allowed to fall below 90% of free feeding weight. The birds were maintained on a 12:12 h light:dark cycle (light onset 0800 hours), at a temperature of 22 ± 2 °C.

The birds were cared for in accordance with Cardiff University's ethical guidelines for animal welfare. At the end of the experiments, the budgerigars were returned to the supplier.

Apparatus

The birds were trained and tested in the holding room in a modified cage (60 × 32 cm and 41 cm high; Fig. 1). Three of the cage sides and the roof were constructed of 1 cm gauge wire mesh; mesh on the fourth side was replaced with a transparent Perspex plate. The base of the cage was covered with sand sheets. The cage could be divided into two chambers of unequal size (37 × 32 cm and 41 cm high; 23 × 32 cm and 41 cm high) using a movable wooden partition. The smaller chamber at the back contained two perches (21 cm off the ground) and was used as a holding chamber for the birds prior to session onset, and between trials during a session. The larger, test chamber contained the test box and one perch (5 cm off the ground, 15 cm from the front of the cage, 5 cm from the test box). Access to both chambers was obtained though a hatch in one of the long walls of the apparatus, on the nearside of Fig. 1a. The same side was screened from view using a black plastic sheet.

The test box, present at all times in the test chamber, consisted of an opaque box (21 × 10 cm and 4 cm high), and was placed on the floor next to the Perspex screen (Fig. 1). The position of the box was such that its long axis ran parallel to the end wall and the perch. The sides and base of the box were composed of thin sheet metal. The removable lid was composed of opaque white plastic. Half the lid, on the left with respect to the observers, was permanently covered by a section of sand sheet (10.5 × 10 cm); the exposed half could be covered with a piece of white card (10.5 × 10 cm).

The test box was filled to a height of 1 cm with millet. Budgerigars could reach the millet though a hole (diameter 3.5 cm) centrally located in the exposed half of the lid. This hole acted as a receptacle for the stopper, which was made from an inverted bottle cap, 0.8 cm deep. The inside of the stopper was lined with a section of a ping-pong ball to create a concave surface and the entire bottle cap and lining was coloured blue using a marker pen. Two wires, attached to the rim of the stopper, crossed at the centre of its upper surface. The stopper could be displaced downwards to gain access to the food. To prevent the stopper being lifted out, two metal arms, consisting of a loop of wire 1 cm long, were attached to the underside of the stopper. When in place, the stopper was supported by a metal ring, 1 cm high, that surrounded the circumference of the hole on the lower surface of the lid. The inside of the ring, in which the plug rested, was lined with a thin layer of Velcro (eye side).

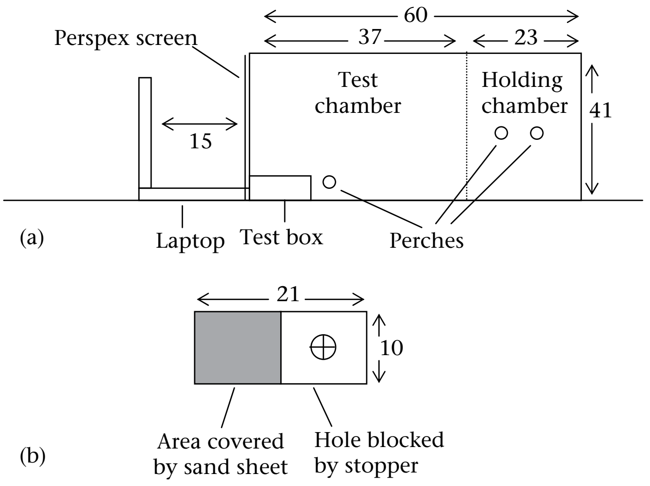

Figure 1. Diagrams showing (a) a side view of the entire apparatus, and (b) an overhead view of the test box. Measurements are in centimetres.

The experimenter, who was positioned, at all times, approximately 1 m from the screened side of the cage, controlled the equipment and collected the data manually. The birds were habituated to the presence of the experimenter during training. All experimental sessions were recorded by an analogue Sony camcorder (model AC-V25A) located behind the laptop. The camcorder was connected to a standard monitor located on a shelf below the test cage, allowing the experimenter to observe the birds indirectly.

Stimuli

During the experiment the observer birds were presented with stimuli consisting of video clips of unfamiliar 'demonstrator' birds making contact with the test box. Three clips were used in total, each lasting 10 s and featuring a different bird flying towards the front of the cage, alighting on the box, and then either feeding through the open hole (magazine training video), or removing a stopper, by pecking (Group Peck video) or stepping (Group Step video), before feeding through the open hole. The pecking and stepping demonstrators each struck the top of the stopper several times with its beak (pecking) or foot (stepping) before the stopper was displaced. To reach the seed on the floor of the box, the demonstrator birds put their heads inside the box. Therefore the pecking behaviour used to pick up the seed was not visible to the camera. However, while feeding, the demonstrators intermittently raised their heads from the box, allowing the camera to capture consummatory beak movements and images of husks falling from the beak.

During filming, the camera was located in front of the test box, in the position of an observer bird approaching the test box from the direction of the holding chamber. Stopper removal clips were chosen for the competence with which the demonstrator removed the stopper, and the clarity with which this could be seen. To enable observers to obtain a clear view of the demonstrator's reward, a small bulb powered by an AA battery was placed inside the test box to light up the millet. This was not present during testing.

The stimuli were recorded using a Sony digital camcorder (model TRV730E) and edited and played back using a Sony laptop with a thin-film transistor screen (model VAIO PCG-FX109K). For software we used DVgate (Sony) and Windows Media Player. Image size was manipulated to make both the filmed budgerigar and the test box appear life size and the background was set to black to minimize visual distraction.

Procedure

The birds were habituated to the apparatus and given magazine training prior to the start of testing. For the first 4 days, millet was made available in the home cage in a plastic box of similar design to the test box (21 × 10 cm and 4 cm high, with two holes in the lid, diameter 3.5 cm). On each of the next 4 days, each bird was placed in the test cage for three periods of 5 min to allow them to habituate to handling and to the cage. The wooden partition was used at the start and end of each of these sessions to restrain the bird briefly within the holding chamber. The test box was present, without the stopper in place, and therefore the birds could feed through the hole in the top of the box.

After the initial 8 days, the birds were placed on a feeding schedule and given a further four to eight magazine training sessions. Each of these sessions comprised 10 trials in which the observer was allowed access to the test box (without the stopper) from the holding chamber while the magazine training video clip (bird feeding from the open hole of the test box) played repeatedly. Each trial lasted 1 min unless the bird fed from the test box, in which case it was allowed 30 s of feeding before the trial ended. At the end of each trial except the last the birds were ushered back into the holding chamber using the cardboard partition. After the last trial they were removed from the apparatus. Birds were moved on to the testing phase of the experiment after four sessions if they had fed in at least 80% of trials in one session. If they had failed to reach this criterion after 4 days, training continued until the criterion was met, or eight sessions had elapsed. If a bird failed to reach criterion after eight sessions it was excluded from the experiment.

Experiment 1a. For the birds in experiment 1a, a test session consisted of 10 observation trials alternated with 10 test trials. Observation trials lasted 1 min. During this time, the 10 s video of a demonstrator removing the stopper and feeding from the test box was presented six times. The test box was present during observation trials, but access to the stopper was prevented by a piece of card placed over the exposed top of the test box. At the end of each observation trial the observer was ushered back into the holding area and restrained there for approximately 30 s using the wooden partition, while the test box was uncovered and the video clip was turned off. The removal of the partition indicated the beginning of a test trial. Test trials ended after 1 min had elapsed or, if the bird removed the stopper, 30 s after the removal response. There were three test sessions, administered on consecutive days.

Experiment 1b. The birds in experiment 1b were given an observation session followed 24 h later by a test session. This sequence was repeated twice over a period of 6 days; the birds observed on days 1, 3 and 5, and were tested on days 2, 4 and 6. During each observation session, two to four birds from a single experimental group were placed in the test cage for 1.5 h while the 10 s video of a demonstrator removing the stopper and feeding from the test box played continuously. The test box was not present during observation sessions. Although they observed in groups, the birds were tested individually. A test session consisted of 10 trials in which the observer was allowed access to the test box while the magazine training video (bird feeding from the open hole of the test box) was shown repeatedly. Test trials ended after 1 min had elapsed or, if the bird removed the stopper, 30 s after the removal response.

Analyses

Data were obtained from 16 of the 24 birds in experiment 1a and from 11 of the 14 birds in experiment 1b. Two birds had to be excluded because their weight was at risk of falling below 90% (one in 1a Group Peck, and one in 1b Group Peck), two because they failed to feed from the test box during magazine training (one in 1a Group Step, and one in 1b Group Peck), and seven because they failed to remove the stopper in any test trial (four in 1a Group Peck, two in 1a Group Step, one in 1b Group Peck). Thus, for the purposes of analysis, the number of birds in each group was: 1a: Group Peck = 7, Group Step = 9; 1b: Group Peck = 4, Group Step = 7. Several of these remaining birds failed to respond in one or two of the three test sessions. Therefore, to preserve statistical power, we combined data from each bird for the three test sessions for analysis.

Videotapes of the observers' behaviour during test trials were scored to provide the data for analysis. Whenever an observer removed a stopper, the method (peck or step) that was used to bring about the removal was recorded. Accuracy was checked by comparing the performance of two independent raters across a randomly selected 30% of test trials. The raters were in agreement regarding the method used for removal in 98.7% of cases.

When a ratio measure is used, scores are limited by the lower bound of 0 and the upper bound of 1, which can result in the distribution of scores being skewed. Therefore, we used analysis of variance (ANOVA) to examine our ratio data; this procedure is known to be robust with respect to deviations from normality (Howell 1992). This parametric approach was chosen, rather than a nonparametric alternative, because the latter would not have been applicable to the results of experiment 2, which included additional within-subjects factors. Experiment 2 sought to replicate, as well as to extend, the results of experiments 1a and 1b, and therefore it was important to apply the same analysis throughout the study.

The data from experiments 1a and 1b were combined for analysis because the birds in these experiments underwent the same preliminary training, observed the same videos of demonstrator behaviour, and were tested using a common procedure. Although the birds in experiment 1b observed their demonstrators over a longer period, and were tested after 24 h rather than immediately after observation, the combined analysis showed that, on average, their discrimination behaviour and response rates did not differ from those of the birds in experiment 1a.

Results and Discussion

Birds making a pecking response would, over trials, either peck at the stopper several times, gradually dislodging it downwards, or exert more continuous downward pressure until the stopper was displaced. In some trials, birds making a stepping response walked over the stopper, in which case their weight displaced the stopper downwards, and in other trials they stood beside the stopper and stamped on it with one foot.

A discrimination ratio was calculated for each bird across all three test sessions by dividing the number of test trials in which it used pecking to remove the stopper by the total number of trials in which the bird removed the stopper using either pecking or stepping. This measure indicates the degree to which a bird showed a preference in favour of pecking (scores between 0.5 and 1) or stepping (scores between 0.5 and 0). A mean discrimination ratio for a single group (or individual) does not provide a valid index of imitation because it cannot be assumed that, in the absence of imitation, the ratio would be 0.5. For example, owing to characteristics of the stopper or other variables in the test environment, budgerigars might find pecking easier than stepping, or vice versa, and therefore their mean discrimination ratio in the absence of imitation might be higher or lower than 0.5. However, it does provide an index of imitation when used to compare groups that have observed different demonstrator actions. For example, a lower mean discrimination ratio in Group Step than in Group Peck would suggest that observation of stepping had promoted stepping and/or that observation of pecking had promoted stepping.

Figure 2, which shows the group mean discrimination ratios for experiments 1a and 1b, indicates that, both when they were tested immediately and when they were tested after a 24 h delay, birds that had observed pecking were more likely than birds that had observed stepping to use pecking to remove the stopper. This was confirmed by an ANOVA in which group (Peck, Step) and experiment (1a, 1b) were between-subjects factors. There was a significant main effect of group ($F_{1,23} = 7.08$, $P = 0.014$; Group Peck: $\overline{X} \pm \text{SEM} = 0.65 \pm 0.10$; Group Step: 0.29 ± 0.09), but the main effect of experiment ($F_{1,23} = 2.12$) and the group*experiment interaction ($F < 1$) were not significant.

The mean total number of removal responses made across the 30 test trials ± SEM was 16.44 ± 1.83. The number of removal responses did not vary across groups: an ANOVA applied to the response rate data failed to indicate a significant effect of group

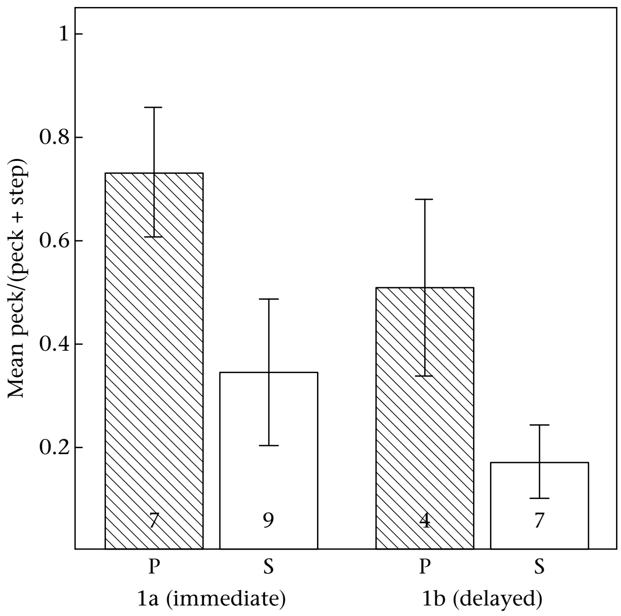

Figure 2. Mean discrimination ratios (peck/(peck + step)) for observers of pecking (P) and stepping (S) in experiments 1a (immediate testing) and 1b (delayed testing). Lines show SEMs. Sample sizes are given within the bars.

($F_{1,23} = 2.86$) or experiment ($F_{1,23} = 3.13$) or a significant group* experiment interaction ($F < 1$).

As indicated above, some birds failed to respond in one of the three tests, and therefore it was not possible to analyse performance across tests in each of experiments 1a and 1b. However, as a basis for comparison with the results of experiment 2, Fig. 3 combines the data from 1a and 1b, showing the mean discrimination ratio for observers of pecking and observers of stepping in each of the three tests. Visual inspection of Fig. 3 suggests that the difference between Group Peck and Group Step did not increase markedly over tests in these experiments.

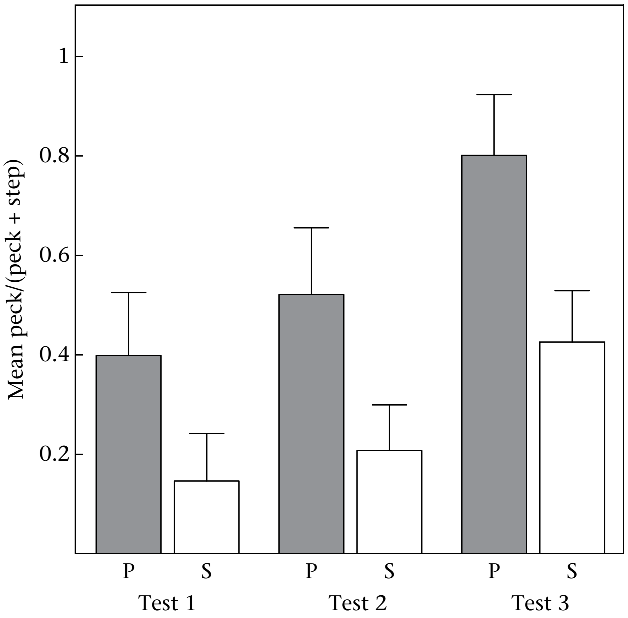

Figure 3. Mean discrimination ratios (peck/(peck + step)) for observers of pecking (P) and stepping (S) for each of the three test sessions in experiments 1a and 1b (combined). Lines show SEM.

Thus, the analysis of mean discrimination ratios provided evidence that birds that saw a pecking demonstrator were more likely to solve the task by pecking than were individuals that saw a stepping demonstrator, and did not indicate that this effect was diminished after a 24 h delay. Addressing the purposes of experiments 1a and 1b, these results suggest that the pecking–stepping imitation effect can be obtained with video stimuli under both immediate and delayed test conditions. However, they cannot be taken to indicate that a delay between observation and testing has no impact on the pecking–stepping imitation effect because the procedures used in experiments 1a and 1b differed in a number of respects. For example, in addition to being tested after a delay, the birds in experiment 1b observed in groups rather than individually, observed for 1.5 h rather than approximately 10 min, and did not receive alternating observation and test trials. One or more of these variables may have increased exposure or attention to the demonstrator's behaviour in the delayed testing groups, obscuring any effect of memory decay or interference.

EXPERIMENT 2

Experiment 2 had three purposes. First, we wanted to replicate the results of experiment 1b. These suggested that the pecking–stepping imitation effect is present when there is a 24 h interval between observation and testing, but they were based on a relatively small sample of birds; in experiment 1b only four observers of pecking removed the stopper on test.

The second purpose of experiment 2 was to investigate the symmetry of the delayed pecking–stepping imitation effect, to find out whether both pecking and stepping are imitated. In principle, the group difference found in experiment 1b, and in previous experiments with immediate testing (e.g. Dawson & Foss 1965; Akins & Zentall 1996; Zentall et al. 1996; Dorrance & Zentall 2001; Nguyen et al. 2005; Saggerson et al. 2005) could have been the result of imitation of pecking, or imitation of stepping, or both of these. To find out, we included a third group in experiment 2, a control group of birds that observed a virtual demonstrator feeding from the test box, but did not observe stopper removal. If budgerigars imitate both pecking and stepping over a delay, then one would expect Group Peck to peck the stopper in a higher proportion of trials than Group Control, and Group Step to peck the stopper in a lower proportion of trials than Group Control. In contrast, for example, if budgerigars imitate pecking but not stepping over a delay, one would expect Group Peck to show a stronger pecking bias than Group Control, and no difference between the biases of Group Step and the controls.

The final purpose of experiment 2 was to reduce the number of birds that failed to remove the stopper in one or more tests so that we could examine the development of the pecking–stepping imitation effect across delayed test sessions. To this end, we made two changes to the test procedure designed to increase the birds' motivation to remove the stopper: Test trials alternated with periods in which the observer could see a virtual demonstrator feeding from the test box, and birds that had failed to respond in two successive test trials were allowed to feed for 30 s from the test box in the absence of the stopper.

Methods

The methods used in experiment 2 differed from those of experiment 1b in the following respects.

Subjects

We randomly assigned 24 naïve budgerigars in equal numbers to Groups Peck, Step and Control. The experiment was conducted in two replications, with half of the birds from each group included in each replication.

Procedure

During the 1.5 h observation period, the birds in Group Control observed the magazine training video, showing a bird approaching and feeding from the open hole in the top of the test box. Group Control did not observe stopper removal. Each of the three test sessions (on days 2, 4 and 6) contained a minimum of 10 test trials. Before each test trial, the bird was allowed to observe a 1 min clip of the magazine training video, in which a demonstrator approached and fed from the hole in the test box six times. If a bird failed to remove the stopper in any two consecutive test trials, it was given a 'magazine trial', that is, allowed access to the test box, with the stopper absent, for 1 min or until it had fed from the box for 30 s. If a bird failed to feed in the first magazine trial, it was given a second magazine trial.

Data were obtained from 20 of the 24 birds. Four birds had to be excluded because, in spite of the introduction of magazine trials, they failed to remove the stopper in one or more of the three test sessions. Therefore, for the purposes of analysis, the number of birds in each group was: Group Peck = 7, Group Step = 7, Group Control = 6.

The two raters were in agreement regarding the method used for stopper removal in 96.2% of a randomly selected 30% of test trials. The response topographies were the same as those in experiments 1a and 1b.

Results and Discussion

A discrimination ratio was calculated for each bird in each of the three test sessions by dividing the number of test trials in which it used pecking to remove the stopper by the total number of trials in which the bird removed the stopper using either pecking or stepping. Figure 4 shows the group mean discrimination ratios for each of the three tests. It suggests that, over test sessions, the observers of pecking developed a stronger bias in favour of pecking than observers of stepping and controls, and that the biases of the latter groups did not differ from one another. These impressions were confirmed by an ANOVA in which group (Peck, Step, Control) and replication (1, 2) were between-subjects factors, and test (1, 2, 3) was the within-subjects factor. There was a significant main effect of test ($F_{2,28} = 7.49$, $P = 0.008$), and a significant test*group interaction ($F_{4,28} = 4.14$, $P = 0.022$). The main effects of group ($F_{2,14} = 1.75$) and replication ($F_{1,14} = 1.37$), and the remaining interactions ($F < 1$), were not significant. As a precaution, a Greenhouse–Geisser correction for sphericity was applied in all cases. Following up the test*group interaction, simple effects analysis confirmed that there was a significant effect of group in test 3 ($F_{2,14} = 5.00$, $P = 0.023$), but not in test 1 ($F_{2,14} = 1.19$) or test 2 ($F < 1$). Post hoc comparisons (Bonferroni method) showed that, in test 3, Group Peck had a higher mean discrimination ratio than Group Step ($P = 0.05$) and than Group Control ($P = 0.04$). Group Step did not have a lower mean discrimination ratio than Group Control (see Fig. 4), as one would expect if the birds were imitating stepping as well as pecking.

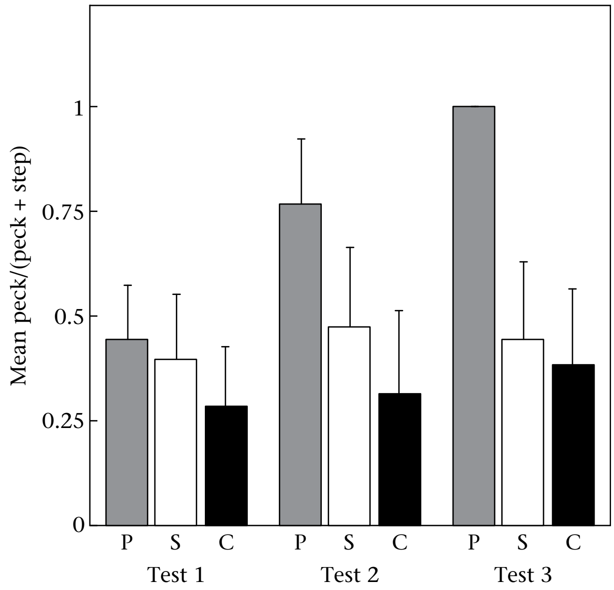

Figure 4. Mean discrimination ratios (peck/(peck + step)) for observers of pecking (P), stepping (S) and controls (C) for each of the three test sessions in experiment 2. Lines show SEMs.

Across test sessions, the mean discrimination ratios recorded in experiment 2 were comparable to those recorded in experiment 1 (Group Peck in experiment 1: $\bar{X} \pm \mathrm{SEM} = 0.65 \pm 0.10$; Group Peck in experiment 2: 0.70 ± 0.13; Group Step in experiment 1: 0.27 ± 0.09; Group Step in experiment 2: 0.44 ± 0.18). An ANOVA applied to these data indicated a significant effect of group ($F_{1,37} = 6.99$, $P = 0.012$) but no effect of experiment or an experiment*group interaction ($F < 1$ in both cases). Numerically, Group Step made proportionally more pecking responses (and therefore fewer stepping responses) in experiment 2 than in experiment 1, but this difference did not approach significance ($F < 1$).

The mean total number of removal responses made across test sessions ± SEM was 27.35 ± 0.62. This response rate is substantially higher than that observed in experiments 1a and 1b, suggesting that the new procedures were effective in increasing motivation. There was strong evidence of variation between groups in the mean number of removal responses ($F_{2,14} = 7.33$, $P = 0.007$): the birds in Group Control ($\bar{X} \pm \mathrm{SEM} = 24.5 \pm 1.23$) removed the stopper less frequently than the birds in Group Peck (28.29 ± 0.61) and in Group Step (28.86 ± 0.55; $F_{2,14} = 7.33$, $P = 0.007$). In combination with the discrimination ratio data, this suggests that, although observation of a virtual demonstrator using stepping to remove the stopper did not influence the observers' choice of response, it did, like observation of pecking, increase the observers' rate of successful stopper removal. Statistical analysis of the number of removal responses, or 'response rates', also indicated that the rate increased over tests (test 1: $\bar{X} \pm \mathrm{SEM} = 8.45 \pm 0.39$; test 2: 29 ± 0.34; test 3: 9.9 ± 0.1; $F_{2,28} = 7.07$, $P = 0.007$), that this tendency was slightly more pronounced in the first replication than in the second ($F_{2,28} = 3.9$, $P = 0.044$), and that the response rate was lower in the first replication (26.27 ± 0.94) than in the second (28.67 ± 0.53; $F_{1,14} = 7.01$, $P = 0.019$). However, variations in response rate cannot explain the effects of group on discrimination ratios reported above. The test*group interaction effect on response rate was not significant ($F_{4,28} = 1.84$), and the number of removal responses made in test 3 did not vary between groups ($F < 1$).

GENERAL DISCUSSION

To investigate the psychological processes mediating the pecking–stepping imitation effect in birds, we used video stimuli of demonstrator behaviour to address two questions about the effect. Does it endure over a 24 h interval between observation and testing? Does it arise from imitation of pecking, imitation of stepping, or imitation of both pecking and stepping? The results of experiments 1a and 1b showed that the effect can be detected using video stimuli, and suggested that the answer to the first question is affirmative. In these experiments, budgerigars that observed pecking showed a stronger pecking bias than budgerigars that had observed stepping, and there was no evidence that the magnitude of this effect varied according to whether the birds were tested immediately after observation or after a 24 h delay. The results of experiment 2 replicated those of experiment 1b and suggested that the delayed pecking–stepping imitation effect arises from imitation of pecking. In their third test session, the birds in this experiment that observed pecking showed a stronger pecking bias than those that observed stepping and than controls that observed an active, feeding conspecific but not stopper removal. The biases of the stepping observers and the controls did not differ.

The endurance of the pecking–stepping imitation effect over a 24 h delay is consistent with the ASL hypothesis, which suggests that imitative behaviour in a novel context will become conditioned to that context. More specifically, it suggests that observation of pecking activates a motor representation of pecking in the observer, and that this becomes associated with cues in the test apparatus. Therefore, on reintroduction to the apparatus, these cues activate the motor representation of pecking and, thereby, overt pecking behaviour. This stimulus–response (S–R) account of the delayed effect found in experiments 1b and 2 is consistent with evidence that observation of pecking and/or stepping facilitates reversal of a conditioned discrimination in birds (Dorrance & Zentall 2002; Saggerson et al. 2005).

An alternative possibility is that the delayed effect was due to response–outcome (R–O) learning during observation. The birds may have learned through demonstrator observation that, in this context, pecking produces food, and therefore made a high proportion of pecking responses when they re-entered the context in the expectation that these would be rewarded (Saggerson et al. 2005). Further experiments, varying the rewards available to the demonstrator, would be necessary to establish whether S–R or R–O learning is responsible for the delayed effect. However, the results of a recent study of the pecking–stepping imitation effect in pigeons make the S–R account more plausible (McGregor et al. 2006). They showed that, when observer birds are tested immediately, the effect was present even when demonstrators responded in extinction, that is, without food reward.

From a methodological perspective it is of interest that, in experiment 2, the delayed imitation of pecking effect emerged across the three test sessions and was reliably detectable only in the third. However, this pattern of emergence does not uniquely identify a developmental process. It is possible that it reflects gradual acquisition of stimulus–response or response–outcome associations (with more rapid acquisition of associations involving pecking than those involving stepping), but it may also reflect perceptual learning about the pecking video stimuli, further learning about the availability of food in the test box, or progressive habituation to the test procedure.

Regarding the symmetry of the pecking–stepping imitation effect, the results of experiment 2 suggested that the delayed effect is due to imitation of pecking and not to imitation of stepping. This is the pattern anticipated by the ASL model on the assumption that the budgerigars in this study had received correlated experience of observing and executing pecking while feeding in groups, and that they had not received, or had received less, of this kind of experience in relation to stepping. This hypothesis could be tested further in two ways. If it is correct, birds that have been deprived of the opportunity to feed in groups should be less likely to imitate pecking, and birds that have received more correlated experience of observing and executing stepping, in the course of their normal development or via explicit training, would be expected to show imitation of stepping.

The failure of experiment 2 to find more stepping in stepping observers than in controls contrasts with the results of a previous study. Using pigeons and an immediate test, Kaiser et al. (1997) reported that more observers of stepping stepped on the target object (a treadle) than did controls that had observed a feeding conspecific. However, this finding is not conclusive because it involved a cross-experimental comparison: the control birds and the stepping observers were tested in different experiments. It is common to find spontaneous, uncontrolled variation in the behaviour of different groups of animals, tested at different times under apparently identical conditions. The effects of replication found in experiment 2 provide an example. Therefore, further research will be required to compare the immediate and delayed effects of stepping observation.

The results of the present study are relevant to the response facilitation hypothesis (Byrne 2002, 2003, 2005; Hoppitt et al. 2007). Like the ASL model, this hypothesis assumes that, for example, the sight of pecking involuntarily activates or 'primes' a motor representation or 'brain record' of pecking. However, unlike the ASL model, the response facilitation hypothesis assumes that the behavioural effects of this priming are always transitory, and that they depend on similarity: the sight of another bird engaging in a behaviour, B, will activate a motor representation of B in the observer to the extent that B looks the same when observed and executed.

Endurance of the pecking–stepping imitation effect over a 24 h delay is inconsistent with the first of these assumptions. A previous study of quail suggested that the pecking–stepping imitation effect can endure over a 30 min interval between observation and testing (Dorrance & Zentall 2001). It is possible that this priming effect could persist for 30 min and still be regarded as 'transitory', but its persistence over 24 h clearly could not be regarded in this way.

Furthermore, because it assumes that priming is similarity based, the response facilitation hypothesis apparently cannot account for the asymmetry that we observed between pecking and stepping. From a third-party perspective, stepping by a demonstrator and stepping by an observer are as alike as pecking by a demonstrator and pecking by an observer. Therefore, if third-party or perspective-independent similarity is what matters, the response facilitation hypothesis would predict imitation of both stepping and pecking. On the other hand, from a first-person (or, more accurately, a first-bird) perspective, 'you stepping' and 'me stepping' are probably more alike than 'you pecking' and 'me pecking'. Therefore, if similarity-based priming is thought to depend on first-person resemblance, the tendency to imitate stepping should be stronger than the tendency to imitate pecking.

It has been known for a long time that, in birds, observation of pecking increases the probability of pecking behaviour (e.g. Turner 1964; Tolman & Wilson 1965), and it has often been assumed that this tendency, described as 'contagion' or 'social facilitation' is innate. The present study does not resolve the question of whether imitative pecking is or is not a result of learning. However, by showing that the effect can persist for 24 h, it does show with some clarity that imitative pecking can result in learning, and thereby give rise to enduring changes in behaviour.

Although experiment 2 found no evidence that the observers imitated stepping, it did show that observers of stepping, like observers of pecking, made more removal responses in total than controls. This suggests that both observation of stepping and observation of pecking support what has been described as 'local enhancement' (Thorpe 1956) or 'stimulus enhancement' (Spence 1937). There are several potential explanations for such an effect (Heyes 1994). For example, observation of action on the stopper may increase attention to, or decrease fear of, this novel object, or, in the present experiment where demonstrators were observed feeding, it may support learning of an association between the stopper and food.

In conclusion, this study has provided the first empirical evidence that the pecking–stepping imitation effect can be obtained in birds with video stimuli, that it endures over a delay of 24 h, and that it is due primarily or exclusively to imitation of pecking. These findings are consistent with the ASL model, which suggests that imitation in birds, and in other species, including humans, depends on correlated experience of observing and executing the same action.

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