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Blind imitation in pigeons, *Columba livia*

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Pigeons that had been trained with a food reward both to peck at and to step on a horizontal plate were allowed to observe a conspecific demonstrator pecking at or stepping on the plate before a test in which the observers were not rewarded for either pecking or stepping. In experiment 1, the demonstrators were not rewarded while being observed. In spite of this, the observers provided evidence of imitation: those that had observed pecking made a greater proportion of pecking responses on test than observers of stepping. In experiment 2, each observer was exposed to a pecking or a stepping conspecific on two occasions. On one occasion, the demonstrator received a food reward for each demonstrated response (continuous reinforcement condition), and on the other the demonstrator's responses were rewarded only rarely (variable interval condition). The observers provided equally strong evidence of imitation in each of these conditions; on test, they made proportionally more of the observed response both when the demonstrators had been richly rewarded and when they had been rarely rewarded. These results show that pigeons engage in 'blind' imitation, that is, their imitative behaviour is not always guided by observational learning about response outcomes.

Research in the last decade has suggested that a range of avian species engage in complex social cognitive and tool-using behaviours (e.g. African grey parrots, *Psittacus erithacus*: Pepperberg 2004; keas, *Nestor notabilis*: Huber et al. 2001; New Caledonian crows, *Corvus moneduloides*: Hunt 1996; Weir et al. 2002; common ravens, *Corvus corax*: Heinrich 2000; Bugnyar & Kotrschal 2002; Western scrub jays, *Aphelocoma californica*: Emery et al. 2004). It has been argued that imitation, copying the topography of observed body movements, requires complex social cognition (Piaget 1962; Meltzoff & Moore 1997), and tasks assessing imitative capacity typically involve the use of tools. It is tempting, therefore, to assume that the substantial number of recent studies showing that birds can imitate body movements provides further evidence of their cognitive sophistication. In the present study we question this assumption.

Recent evidence of imitation in birds has come from two-action tests in which naïve 'observer' animals are first exposed to a trained 'demonstrator' operating on a single object in one of two ways. Each observer is then 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, implies that the subjects copied one or both of the observed actions. In some two-action tests, the object moves through two different trajectories when it is manipulated using the two different response topographies, and therefore demonstrator-consistent responding could be caused by copying of object movements as well as body movements (budgerigars, *Melopsittacus undulatus*: Heyes & Saggerson 2002; Mottley & Heyes 2003; European starlings, *Sturnus vulgaris*: Campbell et al. 1999; Fawcett et al. 2002; pigeons: Klein & Zentall 2003; Japanese quail, *Coturnix japonica*: Akins et al. 2002). Clearer evidence of body movement copying has been provided by two-action tests in which birds that have observed a demonstrator using its beak or its foot to depress a lever or plate subsequently make preferential use of the same effector to depress the object (pigeons: Zentall et al. 1996; Saggerson et al. 2005; quail: Akins & Zentall 1996).

The latest experiments using the beak/foot two-action procedure have begun to investigate what kind of learning mediates the observer birds' tendency to use the same effector as their demonstrator. Given that the movements

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involved are very simple, pecking and stepping, it is very unlikely that birds learn by observation how to perform these movements. For this reason, some investigators prefer to describe copying of pecking and/or stepping as 'response facilitation' (Byrne 2002) or 'mimicry' (Tomasello et al. 1993) rather than imitation. We use imitation in the present study because it is more conventional to do so, and because use of more specialized vocabulary may misleadingly imply that different kinds of body movement copying are known to be mediated by different psychological mechanisms. It is more plausible that they learn during demonstrator observation which of the two actions to use in the experimental situation. Evidence of this kind of learning, which has been described as context imitation (Byrne 2002) and stimulus–response (S–R) learning by observation (Saggerson et al. 2005), comes from two-action experiments showing that demonstrator observation facilitates reversal of a conditional discrimination (Dorrance & Zentall 2002; Saggerson et al. 2005). For example, pigeons that have been trained by conventional means to peck a manipulandum for a food reward in the presence of a red light (i.e. red[peck > food]) and to step on the same manipulandum for a food reward in the presence of a green light (i.e. green[step > food] learn more rapidly to respond correctly to the reverse contingencies (i.e. red[step > food and green[peck > food]) when they have observed a demonstrator responding to the new, reversed contingencies than when they have observed a demonstrator responding to the old contingencies.

These results indicate that the performance of a particular movement pattern can become attached through observation of an action to a feature or features of the situation in which it was performed by the demonstrator. In other words, they show that imitation in birds is context sensitive. Additional studies have investigated whether imitation in birds is also outcome sensitive. They ask whether birds can also learn by observation a response–outcome (R–O) relationship, that an action has certain consequences, and subsequently perform that action with the expectation that it will have those consequences. Children typically begin to show outcome-sensitive imitation when they are 3 years old (Want & Harris 2001).

Indirect evidence of outcome-sensitive imitation in birds comes from studies showing that quail do not imitate pecking and stepping if they are satiated, rather than hungry, when they observe demonstrators performing these actions for a food reward (Dorrance & Zentall 2001) or when they observe demonstrators pecking or stepping in extinction, that is, without reward (Akins & Zentall 1998). These findings are consistent with outcome sensitivity, but they could also be caused by attentional factors. Perhaps delivery of food to the demonstrator simply draws the attention of hungry observers to what the demonstrator is doing. More direct evidence of outcome sensitivity was recently provided by Saggerson et al. (2005, experiment 3) using a devaluation procedure (Adams & Dickinson 1981). In the first phase of this experiment, observer pigeons saw demonstrator pigeons pecking for food illuminated by one colour, and stepping for food illuminated by a different colour, for example pecking for red food and stepping for green food. In the second phase they received experience designed to devalue one of the colours. For example, the observers were given free food to eat in the presence of the red light, but were repeatedly presented with the green light in the absence of food. In the final phase of the experiment the observers were presented with the response plate, and, although neither colour was present and neither pecking nor stepping was rewarded, they performed the action for which the demonstrator had received the devalued outcome less frequently than the alternative action.

The logic of this devaluation experiment is ingenious but, as indicated by Saggerson et al. (2005), the results do not provide conclusive evidence of outcome-sensitive imitation in pigeons. In the first phase of the experiment, when the birds observed pecking for red food and stepping for green food, the observers had the opportunity to learn not only R–O relationships (e.g. that the outcome of pecking is red food and the outcome of stepping is green food), but also S–R relationships (that pecking occurs in the presence of red light and stepping in the presence of green light). Furthermore, if the observer birds learned S–R rather than R–O associations by observation, they would still be expected to show a devaluation effect. Second phase presentation of the green light, in the absence of a demonstrator and of food reward, would be expected to weaken the association between the green light and the stepping response, because stepping elicited by the green light would not be followed by a reward. On the other hand, pecking elicited by presentation of the red light would be followed by a reward. Thus, the green-stepping S–R association would be weakened, leaving the S–R link between the red light and pecking to dominate performance in the final test phase.

Thus, there is firm evidence that birds can learn S–R relationships by observation, that is, they are capable of context-sensitive imitation. However, the evidence that birds can also learn R–O relationships by observation, and thereby engage in outcome-sensitive imitation, is more equivocal. In other words, it is not clear whether birds are capable only of 'blind imitation' (Want & Harris 2002), of copying body movements without knowledge of their outcomes (S–R), or whether they are also capable of goal-directed (R–O) imitation.

We used the beak/foot two-action procedure to investigate further whether pigeons are capable of outcome-sensitive imitation. In contrast with previous studies using this procedure, we examined the effects of action observation, not on acquisition, but on extinction. At the beginning of our procedure, we used conventional means to pretrain each observer bird both to step and to peck in the experimental situation. Stepping and pecking were rewarded in alternating periods of time. Then, once the birds were making both responses with a high frequency for a food reward, we allowed them to observe a demonstrator either pecking or stepping before a test in which the observers were not rewarded for performing either action. This procedure, pretraining followed by extinction testing, may be especially sensitive to the effects of action observation for two reasons. First, pretraining to step and to peck may enhance the observers' capacity to discriminate performance of these two actions. Second, any imitative effect of action observation is measured on a longer and finer scale than is typically the case in acquisition studies. When birds are learning to step and to peck in the experimental situation for the first time, they make relatively few responses of each kind in the test period, and therefore bias in favour of the observed response is measured on a short scale. In contrast, birds that have been pretrained make a relatively large number of responses during an extinction test, and therefore bias in favour of the observed response is measured on a correspondingly longer, more finely delineated scale.

Prior to the extinction test in experiment 1, observer pigeons saw a demonstrator either pecking at or stepping on a response plate in extinction; the demonstrators were not rewarded while being observed, and the observers were not rewarded while subsequently being tested. In this situation, demonstrator-consistent performance would be expected if imitation in pigeons is blind to its consequences, but not if pigeons' imitation behaviour is goal directed. Before the extinction test in experiment 2, observer birds saw a demonstrator pecking or stepping, and being rewarded with food for each response (continuous reinforcement, CRF) or only rarely (variable interval 90 s, VI90). If pigeons engage in blind imitation, they should show an equally strong tendency to imitate in each of these conditions; the demonstrator's schedule of reinforcement should not affect the observers' behaviour. In contrast, if imitation in pigeons is goal directed, one would expect a stronger imitation effect in the CRF condition than in the VI condition.

EXPERIMENT 1

The first experiment compared the behaviour of two groups of observer pigeons, one that had observed a demonstrator pecking a response plate (Group Peck), and one that had observed a demonstrator stepping on the response plate (Group Step). While being observed, the demonstrators for both groups were responding in extinction; they did not receive any food reward. When Akins & Zentall (1998) allowed quail to observe demonstrators pecking or stepping in extinction, they failed to find evidence of imitation. The observer quail tended to use the observed response topography more often than the alternative response topography, but this effect was not statistically significant. We made three changes to Akins & Zentall's procedure, designed to increase the procedure's potential to detect imitation of nonreinforced behaviour. First, we increased the sample size from five to eight birds in each group. Second, we extended the observation period so that each bird observed a demonstrator responding for 10 min rather than 5 min, and witnessed an average of approximately 180 responses. Finally, the observers were given an extinction test rather than an acquisition test. Akins & Zentall's observers had no opportunity to peck at or step on the response plate prior to observing the demonstrator, and they were rewarded with food for each response during the test period. In contrast, prior to observing the demonstrator, our birds had been trained with a food reward to peck at and step on the response plate equally often, and during the postobservation test period we examined the proportion of peck and step responses made by the observers when they were not rewarded for either action. Therefore, if pigeons engage in blind imitation, we anticipated that it would be detected via a tendency for the birds to make proportionally more responses of the type they had observed (pecks for Group Peck and steps for Group Step) than of the alternative type.

Methods

Subjects

The subjects were 16 adult homing pigeons that had previously been used in an observational learning task (Saggerson et al. 2005). In addition, there were four demonstrator pigeons that had previously acted as demonstrators in the study by Saggerson et al. The birds were housed in pairs in cages measuring 55 × 45 × 45 cm, with free access to grit and water. The room temperature was maintained at 19–23 °C and the humidity was 40–60%. The birds were maintained at no lower than 80% of their free-feeding body weight by provision of a restricted amount of food (Pigeon number 1 mix, Lillico, Aylesford, U.K.) after each experimental session. This daily ration was ingested in less than 1 h, but is likely to have remained in the crop for an average of 24 h (C. Walker, Knox Bird Clinic, Australia, personal communication). Each bird's weight and general condition were monitored daily by a member of staff trained in animal husbandry, and weekly by a veterinary surgeon. These inspections indicated that the feeding protocol had no adverse effects on the health of the pigeons. The work was conducted under a Home Office project licence.

The pigeons were maintained in a light-proof room in which the lights were on for 14.5 h each day. Each observer bird was tested at the same time each day, 5–7 days each week, during the period when the lights were on in their holding room.

Apparatus

Demonstrator training and observer testing were carried out in two identical operant chambers (Campden Instruments Ltd, London, U.K.) measuring 35 × 35 × 35 cm (Fig. 1). The left, rear and right walls and ceiling were made of aluminium, and the front door was made of clear Perspex. In the left side wall was a rectangular hole (5 cm wide, 4 cm deep and 6 cm high) through which the pigeon could gain access to seed (New mix conditioning seed, Lillico, Aylesford, u.k.) when the hopper was raised. The other walls and the ceiling were painted white. The floor was constructed of wire mesh beneath which was placed absorbent paper. Ambient illumination was provided by an angle-poise lamp, with a 60-W bulb, placed above the demonstration/test compartment.

The manipulandum was made from an elliptical plastic plate (8.5 × 11.8 cm; gauge: 2 mm). The plate was attached by a metal bar to a microswitch which was set into a circular wooden base (diameter: 9 cm; height: 2 cm). The plate and the base were both painted dark

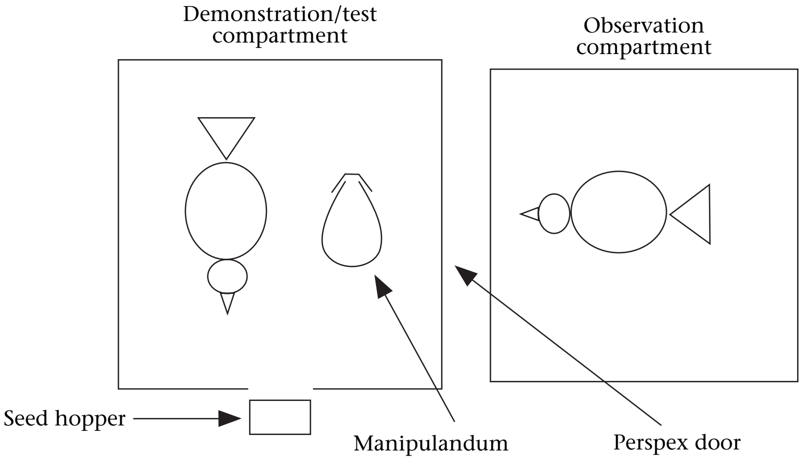

Figure 1. Plan of the apparatus used in experiments 1 and 2.

grey and in their resting states were separated by 1 cm. A shield 3 cm deep fixed around the circumference of the base prevented the plate moving sideways and obscured the lateral view of its depression. Depression of the plate by 5 mm or more tripped a microswitch that started a timer. The timer stopped when the plate returned to its resting state. Short responses (<150 ms) were recorded as pecks, and long responses (>150 ms) were recorded as steps. The chamber was controlled with Arachnid software (Paul Fray Ltd, Cambridge, U.K.) running on an Acorn RISC PC.

The demonstration/test compartment was separated by 8 cm from an observation compartment (30 × 29 cm and 27 cm high) made entirely of transparent Perspex. The observation compartment had a wire-mesh floor beneath which was placed absorbent paper. Observers entered the compartment through a Perspex door in the rear wall, and were able to view the demonstration/test compartment through the transparent Perspex.

Demonstration and test sessions were videorecorded with a colour video camera (Panasonic VHS camera, model NV-M40 HQ), which was positioned 90 cm from the observation chamber so that both the observation and demonstration/test compartments could be recorded through the Perspex walls.

Procedure

Demonstrator training. The four demonstrator pigeons were trained either to peck at or to step on the manipulandum to gain a food reward. Two were trained to peck and two to step. Each session lasted for 30 min. So that the demonstrator birds became accustomed to the presence of another bird, we placed a 'dummy observer' in the Perspex observation compartment in front of the demonstration/test compartment during each demonstrator training session. The dummy observer pigeon used for demonstrator training was not tested in the experiment. Once demonstrators were able to peck or step for food they were placed on increasingly lean variable interval (VI) schedules of reinforcement, until they reliably responded a number of times before a food reward was delivered. By the end of training each demonstrator bird responded on a VI90 schedule. That is, during every second of the session there was a one in 90 chance that food would be delivered if a response was made. During each food delivery, seed was accessible for 3 s. Demonstrators received 25 sessions of training before testing began.

Observer pretraining. Observers were trained both to peck at and to step on the manipulandum to gain a food reward. Each training session lasted for 28 min, divided into four, 7-min periods. During two of these periods, steps were rewarded and pecks were not rewarded (step+), and during the other two periods pecks were rewarded and steps were not rewarded (peck+). Step+ and peck+ periods alternated in the course of each session. Whether a session began with a step+ or a peck+ period was randomized within blocks of two sessions. Thus, birds could distinguish between step+ and peck+ periods only by making a step or peck response and registering whether the response was rewarded. Each observer received 12–22 pretraining sessions (see below).

Observation and testing. After the final pretraining session we assigned each bird to one of two observer groups, Peck or Step. During the test session the observer was placed into the observation compartment and allowed to observe one of the demonstrators either pecking at or stepping on the manipulandum in the demonstration/test compartment for a 10-min period. The demonstrator did not receive any reward during the observation period. We then removed the demonstrator from the demonstration/test compartment and cleaned the manipulandum with a household surfactant (Mr Muscle multisurface cleaner). Immediately after the observation period had finished, we placed the observer bird in the demonstration/test compartment for a 10-min test period in which the number of pecks and steps it made on the manipulandum were recorded. The observer did not receive any reward during the test period.

Because there were only four demonstrator birds and 16 observers, only four observers could be tested on any one day: two from Group Peck, and two from Group Step. During the observation period the demonstrators did not receive any reward. Therefore, to ensure that the demonstrators would respond reliably, we retrained them after each of their observers was tested. Consequently, observer pigeons tested later in the experiment received more pretraining sessions than those tested at the beginning. The first set of observers were tested after 12 pretraining sessions, the second after 14 sessions, the third after 18 sessions and the fourth after 22 sessions. Since there were an equal number of observers from each group in each set, Group Peck and Group Step received equal amounts of pretraining.

Results and Discussion

We converted the birds' peck and step responses into a discrimination ratio (the number of pecks made in a given period divided by the total number of pecks and steps made in the same period). A ratio above 0.5 indicates more pecking than stepping, and a ratio below 0.5 indicates more stepping than pecking. One cannot assume that birds that have not been influenced by their observation experience would have an average ratio of 0.5. It is possible that the baseline ratio is above or below 0.5 because, for example, one of the two responses may require more effort. Therefore, using the standard logic of a two-action test, we assessed the effects of observation experience by comparing the ratios of groups of birds given different kinds of observation experience, rather than by comparing each group's ratio with a hypothetical chance ratio of 0.5.

Using the same apparatus as that used in the present study, Saggerson et al. (2005) showed that the automated response recording system distinguishes steps from pecks with a high level of accuracy. To provide a further check on the validity of the automated measures, we scored the behaviour of the observers, from the video recording, during all test sessions, and compared the discrimination ratios calculated on the basis of this manual scoring with those generated by the automated system. The mean discrimination ratio ± SEM for both groups combined was 0.46 ± 0.03 for the automated scoring system and 0.50 ± 0.05 for the video scoring. There was no significant difference between the two scores (paired *t* test: $t_{30} = 1$, NS).

Demonstrators' behaviour

As intended, while they were being observed the demonstrators for Group Peck made a greater proportion of peck responses (mean discrimination ratio ± SEM = 0.83 ± 0.04) than the demonstrators for Group Step (0.18 ± 0.09; ANOVA: $F_{1,14} = 43.4$, $P < 0.0001$). On average, demonstrators made 183 ± 22 responses during each observation session. The number of responses made by Group Peck and Group Step demonstrators did not differ ($F_{1,14} = 3.25$, NS).

Observers' behaviour

The effectiveness of observers' pretraining was confirmed by analysis of their mean discrimination ratios during the final pretraining session before observation and testing. This analysis showed that the observers made proportionally more peck responses during peck+ periods ($\overline{X} \pm \text{SEM} = 0.70 \pm 0.06$) than during step+ periods (0.24 ± 0.05; ANOVA: $F_{1,14} = 54.9$, $P < 0.0001$), and that the groups did not differ in their pretraining discrimination performance ($F_{1,14} < 1$, NS).

Immediately after observing a demonstrator pecking or stepping without reward, the observers received a test in which neither response was rewarded. We predicted that, if pigeons engage in blind imitation, they would tend to perform the same response as the demonstrator even under these conditions. The test results confirmed this prediction (Fig. 2a). Group Peck made proportionally more peck responses (mean discrimination ratio ± SEM = 0.56 ± 0.07) than Group Step (0.26 ± 0.10; ANOVA: $F_{1,14} = 6.14$, $P = 0.027$). The groups did not differ in the total number of responses made during the test period. On average, Group Peck made 35 ± 8 responses and Group Step made 40 ± 15 responses in total ($F_{1,14} < 1$, NS).

EXPERIMENT 2

Experiment 1 showed that, in an extinction test, pigeons imitate pecking and/or stepping even when they have observed conspecific demonstrators performing these actions without reward. These results suggest that pigeons

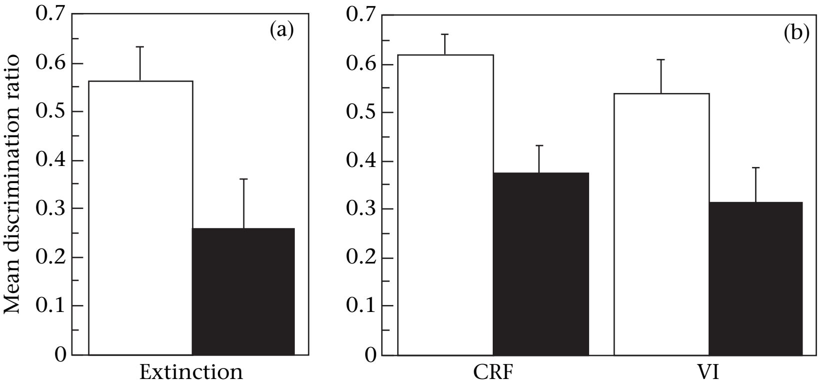

Figure 2. Mean discrimination ratios + SEM for observers in Group Peck (□) and Group Step (■), (a) in experiment 1 after observing a demonstrator pecking or stepping without reward (extinction) and (b) during the continuous reinforcement (CRF) and variable interval (VI) test periods in experiment 2. See text for details.

sometimes engage in blind imitation; they copy observed response topography in the absence of any expectation that performance of the demonstrated action is more likely than performance of the alternative action to have a positive outcome for the actor.

The results of experiment 1 are interesting because previous studies failed to find evidence of blind imitation in birds (Akins & Zentall 1998; Dorrance & Zentall 2002; Saggerson et al. 2005). However, they do not contradict previous reports of goal-directed imitation in birds by implying that the imitative behaviour of birds is always blind to its consequences. It is possible that birds engage in blind imitation only under the conditions represented in experiment 1, when they have observed a demonstrator responding in extinction, and they are themselves tested in extinction. For example, mechanisms that are sensitive to the outcomes of observed actions may be active when the demonstrator is rewarded, but not when the observation and test environments both indicate that reward is no longer available.

Thus, whereas in experiment 1 we asked whether pigeons will imitate when their observation experience indicates that there is no prospect of reward, in experiment 2 we addressed a different and more subtle question. Do pigeons imitate more when they have observed a demonstrator's behaviour richly rewarded than when they have observed it rarely rewarded? To find out, we conducted a further experiment with the birds from experiment 1. After a period in which we retrained the birds to peck at and to step on the response plate with approximately equal frequency, each observer underwent two extinction tests. Prior to one of these tests they observed a demonstrator pecking or stepping with continuous reinforcement (CRF); each peck or step response was followed by delivery of food to the demonstrator. Before the other test, the observer pigeons saw a demonstrator pecking or stepping on a variable interval 90-s (VI90) schedule; a food reward was delivered to the demonstrator after the first peck or step response made after an average interval of 90 s had elapsed since the last delivery. The demonstrators made the same number of responses while being observed on CRF and on VI. Thus, in the CRF condition, the observers had the opportunity to learn that either pecking or stepping was richly rewarded, and in the VI condition they had the opportunity to learn that either pecking or stepping was rewarded only rarely. If imitation in pigeons is sensitive to the frequency with which observed behaviour is rewarded, one would expect a stronger imitation effect in the CRF condition than in the VI condition. In contrast, if imitation in pigeons is blind to the frequency with which observed behaviour is rewarded, one would expect an imitation effect of equal magnitude to occur in each condition.

Methods

Subjects

The same birds were used in experiment 2 as in experiment 1. Group assignment was counterbalanced across experiments: half of each group in experiment 1 was assigned to Group Peck in experiment 2, and the other half of each group in experiment 1 was assigned to Group Step in experiment 2. One of the stepping demonstrators failed to make proportionally more steps than pecks during retraining and was excluded from the experiment. To equate the groups, we therefore used one demonstrator for Group Peck and one for Group Step.

Procedure

The procedure was the same as that of experiment 1 with the following exceptions. Demonstrators were trained for 12 sessions before testing began. Prior to testing, observers received 18 pretraining sessions. During each test session the observer was placed in the observation compartment and allowed to watch its demonstrator either pecking or stepping on the manipulandum 150 times. The observation period then terminated and the experimenter removed the demonstrator. He placed the observer in the demonstration/test compartment and recorded the number of pecks and steps made to the manipulandum for a 10-min period. The observers' responses were not rewarded during the test period.

Each observer completed two test sessions. Prior to the first test session, half of the observers saw the demonstrator receive a food reward after every response (CRF condition) and half saw the demonstrator receive a food reward at intervals averaging 90 s (VI condition). In the VI condition, as in the CRF condition, the reward was delivered immediately after the demonstrator had made a response. After the first test session, observers received three further sessions of pretraining to recover previous levels of responding before we conducted a second test session. Those observers that saw the demonstrator responding on CRF prior to the first test session saw the demonstrator responding on the VI schedule prior to the second test and vice versa for observers tested first in the VI condition. Thus, the order of testing in CRF and VI conditions was fully counterbalanced.

Results and Discussion

Demonstrators' behaviour

The demonstrators were required to make 150 trained responses while being observed. The mean discrimination ratio ± SEM was 0.97 ± 0.01 for the peck demonstrator and 0.04 ± 0.02 for the step demonstrator. The mean number of reinforcers delivered to the demonstrators ± SEM was 78.6 ± 4.1 in the CRF condition and 3.3 ± 0.7 in the VI condition. (The demonstrators did not receive 150 reinforcers in the CRF condition because they tended to double-peck and double-step, that is, to make two responses in quick succession, such that the first could not be rewarded before the second occurred.) The demonstrators' response rates did not vary between conditions. On average, the 150 responses were completed in 439 s in the CRF condition and in 587 s in the VI condition (ANOVA: $F_{1,15} = 1.18$, NS).

Observers' behaviour

The effectiveness of observers' pretraining was confirmed by analysis of their mean discrimination ratios during the final pretraining sessions before observation and testing. This analysis showed that the observers made proportionally more peck responses during peck+ periods ($\overline{X} \pm \text{SEM} = 0.77 \pm 0.06$) than during step+ periods (0.32 ± 0.05; ANOVA: $F_{1,14} = 61.0$, $P < 0.0001$), and that the groups did not differ in their pretraining discrimination performance ($F_{1,14} < 1$, NS).

The results of principal interest were from the test sessions after observation of CRF and VI performance (Fig. 2b). These indicated that the observer pigeons showed equally strong tendencies to imitate richly rewarded and rarely rewarded demonstrators. An ANOVA in which condition (CRF, VI) was the within-subjects variable and group (Peck, Step) was the between-subjects variable showed a significant main effect of group ($F_{1,14} = 9.01$, $P < 0.01$), but neither the main effect of condition ($F_{1,14} = 2.92$, NS), nor the group * condition interaction ($F_{1,14} < 1$, NS), was significant. Simple effects analysis confirmed that observers of pecking made a greater proportion of peck responses than observers of stepping both in the CRF condition (Group Peck: $\overline{X} \pm \text{SEM} = 0.62 \pm 0.04$; Group Step: 0.38 ± 0.06; ANOVA: $F_{1,14} = 11.4$, $P = 0.005$) and in the VI condition (Group Peck: 0.54 ± 0.07; Group Step: 0.32 ± 0.07; $F_{1,14} = 4.8$, $P = 0.05$).

If pigeons' imitative behaviour was sensitive to the presence or absence of demonstrator reward, but not to the frequency with which the demonstrator is rewarded, then one would expect the birds in experiment 2 to have shown a stronger imitation effect than those in experiment 1 but we found no indication of such an effect (Fig. 2). However, to examine this possibility further we performed an additional statistical analysis involving the eight birds that observed the same response type (pecking or stepping) in experiment 1 and in the CRF test in experiment 2. We assessed the imitative behaviour of each bird in each test by using a 'matching discrimination ratio', calculated by dividing the number of responses that were the same as those of the demonstrator (pecks if the demonstrator was observed pecking and steps if the demonstrator was observed stepping) by the total number of responses made on test. The mean matching discrimination ratio in the CRF test ± SEM was 0.63 ± 0.06 and in the extinction test 0.72 ± 0.10, which did not differ (paired samples t test: $t_7 = 0.95$, NS). Thus, there was no evidence that the pigeons were more likely to imitate when they had observed a demonstrator being rewarded than when they had observed a demonstrator responding in the absence of reward.

Although the demonstrators' schedule of reinforcement did not affect the observers' tendency to imitate in experiment 2, analysis of response frequencies indicated that the observers were sensitive to this variable. Observers made more responses after observing a demonstrator responding with continuous reinforcement than after observing a demonstrator responding on a VI schedule (ANOVA: $F_{1,14} = 8.9$, $P = 0.01$). Group Peck and Group Step did not differ in response frequency ($F_{1,14} = 2.1$, NS), and the group * condition interaction was not significant ($F_{1,14} < 1$, NS). On average, Group Peck made 98 ± 18.9 and Group Step 108 ± 21.8 responses in the CRF test, whereas Group Peck made 35 ± 7 and Group Step 69 ± 12 responses in the VI test.

Thus, it appears that observation of a demonstrator receiving continuous reinforcement promotes a higher overall rate of responding than observation of a demonstrator receiving a food reward occasionally. This suggests that the sight of a conspecific feeding had a generalized activating or arousing effect on the observers. However, we found no evidence that observation of intermittent reinforcement was less likely than observation of continuous reinforcement to promote imitation of the topography of the demonstrators' behaviour.

GENERAL DISCUSSION

Research using two-action tests has begun to investigate the kinds of learning that mediate imitation in birds. Previous work on this topic has provided compelling evidence of S–R learning by observation in birds. It has shown, using conditional discrimination procedures, that observation of a demonstrator bird performing a response, R, in a particular stimulus context, S, results in the observer forming an S–R association, making the observer more likely to perform R than an alternative response in the presence of S (Dorrance & Zentall 2002; Saggerson et al. 2005). Imitation arising from an S–R association could be blind; exposure to the S could elicit performance of imitative behaviour without the observer having any expectations about the outcome of that behaviour. Alternatively, it could be goal directed, mediated by observational learning about response–outcome (R–O) relationships. Previous studies have provided some evidence of R–O learning by observation in birds, but their findings were not conclusive (Dorrance & Zentall 2001; Saggerson et al. 2005).

Our results indicate that pigeons engage in blind imitation, and provide no evidence of goal-directed imitation in these birds. Examining the effects of observing pecking or stepping on extinction of these behaviours, we found that pigeons imitate behaviour performed in the absence of reward (experiment 1), and that they are equally likely to imitate richly rewarded and rarely rewarded behaviour (experiment 2). These findings imply outcome insensitivity rather than goal directedness. They suggest that the observer birds in our experiments either did not learn by observation about response outcomes, or that such learning occurred but did not have a significant impact on the observers' behaviour.

Our results suggest that imitation in pigeons can be insensitive or 'blind' with respect to extrinsic rewards. In principle, such behaviour could still be 'intrinsically reinforcing'; pigeons may enjoy doing it. However, in the absence of an independent measure of intrinsic reinforcement, such as an assessment of whether pigeons are willing to work for the opportunity to imitate response topographies, an intrinsic reinforcement hypothesis would be highly speculative.

It is possible that the imitative behaviour of pigeons, or of birds more generally, is always blind, that is, it is never goal directed. As indicated in the Introduction, alternative explanations are available for findings that have been interpreted as evidence of goal-directed imitation in birds. For example, in an acquisition test, quail do not imitate pecking and stepping if they are satiated, rather than hungry, when they observe demonstrators performing these actions for a food reward (Dorrance & Zentall 2001). This may indicate that quail are sensitive to the outcomes of demonstrators' actions, or it may reflect a tendency among quail to attend more closely to the actions of conspecifics when they are hungry than when they are satiated.

Alternatively, imitation in birds may be blind in some conditions and goal directed in others. If this is the case, a priority for further research will be to identify the conditions in which each kind of imitation occurs. In combination, the results of the present study show that pigeons may engage in blind imitation when they observe both unrewarded (experiment 1) and rewarded behaviour (experiment 2). In contrast with some previous studies reporting evidence of goal-directed imitation in birds (Akins & Zentall 1998; Dorrance & Zentall 2001), we used extinction rather than acquisition tests. This contrast raises the possibility that blind imitation is more likely when observer birds have already learned to perform the observed behaviours in the target context, and that goal-directed imitation is more likely when they have not. However, Saggerson et al. (2005) found evidence of goal directedness with an extinction test, implying either that their devaluation effect was due to S–R rather than R–O learning, or that there is a more complex set of variables determining whether avian imitation is blind or goal directed.

Determining the conditions in which imitation is blind and those in which it is goal directed or outcome sensitive is also important from a functional perspective. Theoretical analyses of the evolution of social learning indicate that copying the behaviour of others (whether through imitation or some other process of social learning) is not an adaptive strategy when applied indiscriminately (Boyd & Richerson 1995; Giraldeau et al. 2002). To increase the mean fitness of individuals in a population, copying should be more likely under conditions where it is probable that the demonstrator has better information than the observer. Laland (2004) has distinguished a variety of social-learning strategies that would have this effect, for example, 'copy the majority', 'copy successful individuals' and 'copy when uncertain'. In demonstrating blind imitation, our results suggest that the imitative behaviour of these birds is not consistently well tuned to the success of their demonstrator's behaviour.

Whether it is blind or goal directed, imitation of response topography requires the translation of visual input from a demonstrator's behaviour (e.g. the sight of another bird stepping) into motor output (e.g. stepping behaviour by the observer). The Associative Sequence Learning (ASL) model of imitation suggests that this translation is achieved through associative learning (Heyes & Ray 2000; Heyes 2003). This model proposes that animals acquire the capacity to imitate particular behaviours through experience of concurrently observing and executing those behaviours. For example, a bird will be able to imitate stepping to the extent that it has previously engaged in stepping behaviour while observing the stepping behaviour of other birds. In accordance with standard principles of associative learning, such experience of behavioural synchrony establishes an excitatory link between a visual and a motor representation of stepping behaviour. Once this 'vertical link' is in place, observation of stepping will activate the visual representation of stepping, and this excitation will be propagated to the motor representation, increasing the probability that the animal will perform the observed behaviour.

The ASL model has received empirical support from research on imitation in humans (e.g. Heyes & Ray 2004; Heyes et al. 2005; Bird & Heyes 2005; Brass & Heyes 2005) and in birds (Hoppitt 2005; Saggerson et al. 2005). The bird studies have shown that the levels of behavioural synchrony occurring spontaneously among domestic fowl, *Gallus gallus domesticus*, are sufficient to support the establishment of vertical links for, and therefore imitation of, a range of behaviours (Hoppitt 2005). They have also supported the hypothesis that observation of behaviour immediately activates a motor representation of the observed behaviour by showing that pigeons imitate stepping and pecking, not only in a postobservation test, when they have access to a response plate, but also while observing their demonstrators (Saggerson et al. 2005).

Byrne (2002, 2003, 2005) has proposed that translation of visual input from a demonstrator's behaviour into motor output may be achieved through 'response facilitation'. At the descriptive level, response facilitation is a phenomenon in which the probability that an animal will perform a response already in its repertoire is increased by observation of another animal performing that response. The hypothetical mechanism mediating response facilitation is priming of brain records. It is assumed that, when observed responses are transparent, that is, the sensory input received during observation and execution of the action are similar (Heyes & Ray 2000), observation of the response will activate a psychological representation or 'record' of the action, and that this increases the probability that the action will be performed.

The ASL and response facilitation hypotheses are convergent in many respects. For example, they both assume that observation of behaviour can lead to activation of motor representations or records in the absence of reward, and that neural tissue with mirror properties (although not necessarily 'mirror neurons', Byrne 2005; Heyes 2005) mediates this effect. However, whereas the ASL model attributes the potential for priming of motor representations to learned associations between sensory and motor representations, the response facilitation hypothesis assumes that priming does not depend on learning, and that it occurs by virtue of the similarity between sensory and motor representations. Consequently, response facilitation is expected to occur only for relatively transparent actions, and its effects are thought to be of limited duration. Neither of these features fits well with our results. First, stepping and pecking are each relatively opaque rather than transparent actions; they yield disparate sensory feedback when observed and executed. For example, neither the demonstrator nor the observer pigeons in this study typically looked at their feet while stepping. Therefore, when a bird observed stepping he saw the whole body of a conspecific rise and one of its feet make contact with a horizontal plate, but when a bird performed a stepping movement he simply obtained a more elevated view of the area of the apparatus at which he was looking. Second, although in the present study we did not investigate the duration of the imitative effect, previous experiments have shown that imitation of stepping and pecking in birds occurs over intervals of 30 min (Dorrance & Zentall 2001) and 22 h (Richards 2003).

Many commentators have assumed that imitation in nonprimate species is blind, and therefore dismissed it as nothing more than 'instinctive imitation' (Morgan 1900), 'mimicry' (Tomasello et al. 1993) or 'response facilitation' (Byrne 2002). Our results do not support the view that imitation in primate and nonprimate species is mediated by different mechanisms. However, as far as we are aware, they do provide the first experimental demonstrations of blind imitation in birds, and thereby indicate that caution is necessary in interpreting imitation in birds as evidence of complex social cognition.

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