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Stimulus learning and response learning by observation in the European starling, in a two-object/two-action test

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Juvenile European starlings, *Sturnus vulgaris*, were allowed to observe a conspecific demonstrator using its beak to remove one of two distinctively coloured objects (i.e. a red or a black plug) from a hole in the lid of a plastic box. Both plugs could be removed by either pulling up on a loop of string inserted through the centre of the plug, or pushing down on the plug. When subsequently allowed access to the plugs, and rewarded with food for all removal responses, regardless of the object to which they were made and their direction, observer birds removed the same plug in the same direction as their demonstrator. These results suggest that the two-object/two-action paradigm is a valuable procedure for testing for the simultaneous effects of learning about a stimulus and a response, an object and an action, through conspecific observation.

Social learning refers to learning that occurs as the result of observation of or interaction with another animal (typically a conspecific) or its products (Heyes 1994). Different varieties of social learning can be distinguished on the basis of what a naïve animal learns during its interaction with a demonstrator. In imitative social learning, the naïve animal learns responses, actions, or patterns of behaviour. This form of social learning has been called true imitation (Thorpe 1956) or observational learning (Hall 1963). In nonimitative social learning, the naïve animal learns about the presence, location, and/or value of stimuli, objects, or events in the environment. Local and stimulus enhancement (Spence 1937; Thorpe 1956), for example, occur when a naïve animal is attracted to the site at which a conspecific was behaving or the object, or type of object, with which it has been interacting. Observational conditioning (Cook et al. 1985; Heyes 1994), on the other hand, is the result of learning, by observation, about a relationship between a given stimulus or event and reinforcement.

Attempts to demonstrate imitative learning in nonhuman animals have typically involved allowing naïve animals to watch conspecific demonstrators performing an action on an object for a food reward: these observers subsequently acquired the same response faster than control animals exposed to the mere presence of a conspecific (e.g. Huang et al. 1983). However, this kind of effect cannot be attributed with confidence to true imitation because it may be due instead to local enhancement or to observational conditioning. Observation of the demonstrator's activity may have drawn the observer's attention to the location of the object, making the observer more likely to approach and manipulate the object than if it had not seen the demonstrator. Alternatively, observers may have learned about the relationship between movement of the object and the delivery of food.

Duplicate-cage procedures (e.g. Warden & Jackson 1935; Zentall & Levine 1972; Levine & Zentall 1974), in which a naïve animal is allowed to watch a demonstrator operating a manipulandum for a food reward, while provided with simultaneous access to its own manipulandum, have been used to control for the effects of local enhancement. If, under these conditions, the observer's attention were drawn to the site of its demonstrator's activity, then this would be expected to retard the observer's ability to learn about its own manipulandum. However, if the two manipulanda are sufficiently similar, then any preference an observer might have for its demonstrator's manipulandum would be expected to generalize to its own through stimulus enhancement (Spence 1937).

One procedure used to control for the effects of local enhancement, stimulus enhancement and observational conditioning is the two-action test (e.g. Galef et al. 1985; Heyes et al. 1992), in which a naïve animal is allowed to

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observe a demonstrator performing one of two alternative actions on a single manipulandum. Heyes et al. (1992), for example, found that naïve rats, *Rattus norvegicus*, that were allowed to observe conspecific demonstrators pushing a joystick to the left or to the right for a food reward, subsequently pushed the joystick in the same direction, relative to their own bodies, as had their demonstrators, even when the position of the joystick was rotated through 90° between observation and testing.

These results were interpreted as providing strong evidence of imitative learning in rats (Heyes 1996). Observation of left- and right-pushing demonstrators should have rendered the joystick equally attractive. Therefore, it is difficult to see how local or stimulus enhancement could account for the observers' directionally biased responding. Furthermore, observer rats tested with the joystick in the perpendicular position pushed the joystick in the same direction as their demonstrator, even though this resulted in the joystick moving towards a different point in space to that to which it had moved during observation. This suggests that the effect was not due to observational conditioning, that is, the observers had not merely learned through observation a relationship between movement of the joystick and reward.

Subsequent studies, however, have cast doubt upon the magnitude and provenance of the bidirectional control effect. A meta-analysis of bidirectional control data has indicated that, at the current parameters, the size of the effect is small (Gardner 1997), and there is evidence that rats in the bidirectional control procedure are influenced by odour cues deposited on the manipulandum by demonstrators (Mitchell et al., in press). This raises the possibility that scent-mediated local enhancement, instead of or in addition to response learning by observation, is responsible for demonstrator-consistent responding in this procedure.

Two recent studies using pigeons, *Columba livia* (Zentall et al. 1996) and Japanese quail, *Coturnix japonica* (Akins & Zentall 1996) appear to provide more compelling evidence of imitation. Naïve birds were allowed to observe a conspecific demonstrator either pecking at or stepping on a treadle for a food reward. Zentall et al. (1996) found that when subsequently allowed access to the treadle on test, five of the 10 pigeons that observed pecking pecked at the treadle and five stepped on it. Of the 10 pigeons that observed stepping, nine stepped on the treadle and none pecked at it. In the quail study, Akins & Zentall (1996) reported that birds that observed pecking demonstrators made more pecking than stepping responses. However, birds that observed stepping demonstrators did not make significantly more stepping responses.

The two actions employed in these experiments had the same effect upon the manipulandum. Therefore, these results cannot be explained by the observers learning by observation a relationship between movement of the treadle and food. However, while these experiments provide good evidence that observation of pecking promotes pecking in both pigeons and quail, evidence for a similar effect of stepping is not strong. This raises the possibility that pecking was acquired as the result of nonimitative processes such as contagion and local enhancement. Observation of a pecking demonstrator may have acted as an innate releaser of pecking in an observer (Thorpe 1963). Furthermore, the demonstrator's activity may have rendered the treadle attractive, resulting in the observer directing most of its pecking towards the treadle. To avoid the problem of confounding true imitation with contagious behaviour, the action to be copied in studies of imitative learning should be sufficiently novel or improbable (Thorpe 1963; Zentall 1988).

Unfortunately, two further studies which could have provided evidence against the contagious behaviour hypothesis yielded ambiguous results. First, Kaiser et al. (1997) found that pigeons that observed either a passive conspecific or a conspecific that had been trained to eat from a feeder were less likely to step on a treadle than those birds that observed stepping demonstrators in Zentall et al.'s (1996) original study. However, this difference between experiments might have been the result of local or stimulus enhancement. In Kaiser et al.'s study, the pigeons did not have their attention drawn towards the treadle, and were therefore probably less likely to direct any of their behaviour to the treadle on test. In the second study, Akins & Zentall (in press) found that quail that observed unrewarded stepping made fewer stepping responses than quail that observed demonstrators stepping on a treadle and being rewarded with food, but this difference was not reliable.

The two-action test has also been used with several primate species. For example, in a study by Whiten et al. (1996) chimpanzees, *Pan troglodytes*, observed a human demonstrator opening the lid of a transparent box and removing a piece of food from inside. When closed, the lid was held in place by a pair of bolts that could be removed using one of two actions: the bolts could either be twisted or poked out of the rings through which they passed. When allowed access to the box on test, chimpanzees used the same action as their demonstrator had used in order to remove the bolts. However, in this experiment the two actions used by the demonstrators had different effects on the bolts. Twists caused the bolts to rotate in a clockwise direction, while pokes did not cause the bolts to rotate. Furthermore, whereas twists caused the bolts to move towards the demonstrator, pokes resulted in the bolts moving away from the demonstrator. This, Whiten et al. (1996) suggested, raises the possibility of emulation learning (Tomasello 1990). Rather than learning about their demonstrator's actions, chimpanzees may have learned about movement of the bolts.

The question of whether any given social learning procedure involves learning about stimuli or learning about responses is apparently unlikely to receive an unequivocal answer. Exposure to a demonstrator is likely to result in some combination of both of these types of learning, the exact combination depending upon the prevailing conditions. Therefore, any procedure that permits the simultaneous testing for stimulus learning by observation (stimulus enhancement, observational conditioning or emulation learning) and response learning by observation (imitation or observational learning) would be valuable for investigating the relative importance of these two types of learning and the conditions that favour each. In the present study, we used a two-object/two-action test (e.g. Ray 1997) to achieve this objective.

Each subject observed a demonstrator using its beak to remove one of two distinctively coloured objects, a red or a black plug, from a hole in the lid of a plastic box. Half of the subjects observed a demonstrator that had been trained to remove the plug by pulling up on a loop of string inserted through the centre of the plug while the other half observed a demonstrator pushing down on the plug. Observer birds were then allowed access to the plugs for the first time and rewarded with food for all responses, regardless of the object to which they were made and their direction. We expected observer birds to provide evidence of stimulus learning by observation by removing the same plug as their demonstrator, and of response learning by observation by removing the plug in the same direction as their demonstrator.

METHODS

Subjects

We used 48 juvenile European starlings, *Sturnus vulgaris*, of unknown sex, decoy trapped on a pig farm in Somerton, Somerset. Of these, 16 were randomly assigned the role of demonstrator and 28 were observers. We conducted the experiment in two replications, and the remaining four animals served as observers in the first replication, and then as demonstrators in the second. The starlings were caught in June and held in captivity for 1 week before the experiment. After the experiment, they were released back into the wild.

Throughout the experiment, demonstrator and observer birds were housed separately in groups of eight in 2-cm-gauge wire-mesh cages (120 × 66 cm × 41 cm high), with free access to water. Food spillage and waste was collected by a strip of black tar paper, supported by a sheet of wood, beneath the floor of the cage. One hour prior to the start and during the course of experimental sessions, all the birds were food deprived. At all other times, food (high-protein chick crumbs) was freely available. The birds were maintained on a 16:8 h light:dark cycle (light onset 0600 hours), at a temperature of 17–18°C.

Apparatus

All the birds were trained and tested in two cages, identical to the cages in which the birds were housed. Each cage (see Fig. 1) was divided into two chambers of equal size (60 × 66 cm 41 cm high) by a wooden partition, and each chamber was further subdivided by a wire-mesh partition to form two compartments of equal size (30 × 66 × 41 cm). The left compartment of each chamber was used for demonstration and testing, and the right housed the observer. Access to both compartments could be gained by way of separate doors located at the front of the cage. A single perch, extending from the front to the back of the cage and located ca. 6 cm from the ceiling and 3 cm from the right wall, was provided in each compartment.

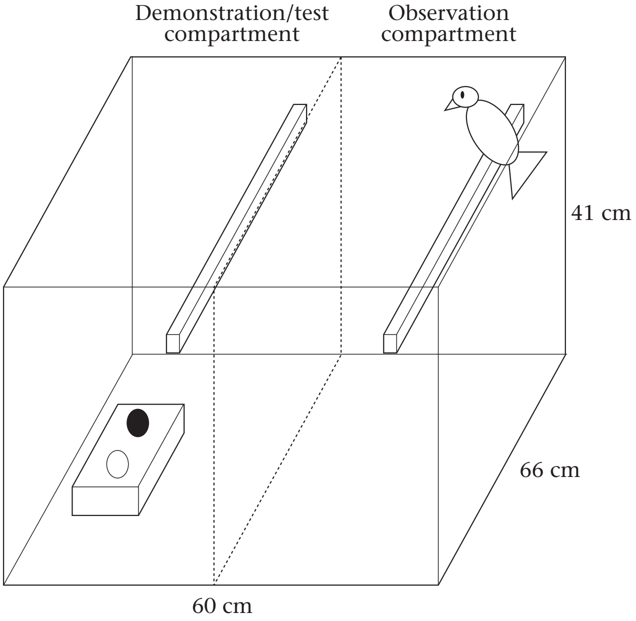

Figure 1. Schematic representation of the apparatus showing the position of the wire-mesh partition (dotted square) and food box. The filled circle shows the position of the black plug and the open circle shows the position of the red plug.

In the demonstration compartment, a clear plastic box (14.5 × 9.5 × 5.5 cm) was placed on the floor next to the wall directly opposite the wire-mesh partition (see Fig. 1). The position of the box was such that its long axes ran parallel to the adjacent sidewall. A piece of white card (19 × 14 cm) was secured to the lid of the box, and the entire box was placed inside an open-top white cardboard container (19 × 14 × 6 cm). This container was also used to cover up the plastic box when it was not in use.

The plastic box was divided into two equal sections (7.25 × 9.5 × 5.5 cm) by a sheet metal partition, in order that either or both compartments could be filled with live mealworms, *Tenebrio molitor*. The mealworms could be reached via two separate holes (diameter 3.5 cm) in the lid of the food box, one directly above the centre of each section. These holes served as receptacles for the plugs, which were made from inverted bottle caps, 1.3 cm deep. The inside of each bottle cap was lined with a section of ping-pong ball to create a concave surface, and the entire bottle cap and lining was coloured with either a red or a black odourless marker pen. A loop of string, 2 cm long, was inserted through a small hole in the centre of the cap and secured with a knot. When in place, the red plug was always in the hole nearest the front of the cage, and the black plug in the hole nearest the back of the cage. Both plugs could be removed from their receptacle by either pulling up on the loop of string inserted through the centre of the plug, or by pushing down on the centre of the plug.

When in place, the plugs were 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 sponge. For the purpose of demonstrator training, three brackets, positioned equidistant from one another, were secured to the free end of the metal ring and could be moved directly underneath the hole such that the plug could not be pushed downwards. Three metal brackets were also secured to the base of the plug, so that when the plug was in place and the brackets were positioned pointing away from it, the plug could not be pulled upwards.

The equipment was controlled, and the data were collected manually, by the experimenter, who was positioned, at all times, ca. 30 cm from the front of the cage and visible to the subjects. Demonstrator and observer birds rapidly habituated to the presence of the experimenter over the course of training. Their behaviour in the presence of the experimenter was not detectably different from their behaviour when observed from behind a door through a peephole. All experimental sessions were recorded by a JVC camcorder (Model number GR-AX60E), supported on a tripod immediately in front of the experimenter.

Procedure

Each session began when the cardboard container covering the food box was removed, and finished once a bird had made 10 rewarded responses or a certain period of time (variously defined below) had elapsed, at which point the food box was re-covered.

Demonstrator training

Sixteen demonstrator birds received three daily sessions of training to feed from the plastic box. The first training session was conducted in the demonstrators' home cage in the presence of its cagemates, and the last two sessions with each bird, on its own, in the demonstration compartment of the experimental chamber. During session 1, demonstrators were allowed to feed from the plastic box, from which the lid had been removed, for 240 min. The lid was replaced during sessions 2 and 3, and each bird was allowed to feed through the holes in the lid of the box for 30 min. During this pretraining period both halves of the food box were filled with mealworms, and the birds were not exposed to the plugs.

After learning to eat from the box, eight of the birds were trained by the method of successive approximation to remove the red plug from the food box. We trained half of these animals to remove the plug by pulling up on the loop of string inserted through the centre of the plug, and half by pushing down on the centre of the plug. The remaining eight animals were trained to remove the black plug, half by pulling up on the loop of string and half by pushing down on the plug. Thus, there were four groups of demonstrators: red up, red down, black up and black down. There was one training session a day and each session lasted until a bird had made 10 rewarded responses or 20 min had elapsed.

During the initial phases of this instrumental training, only the designated plug was inserted in the lid of the food box, and only the compartment below this plug was filled with mealworms. We gradually increased the amount of displacement necessary to remove the plug from its receptacle until each demonstrator was removing a fully inserted plug. Each time the plug was removed using the correct response topography the demonstrator was allowed to take one to three mealworms from the box. The experimenter then retrieved and replaced the plug. Once a demonstrator was reliably removing the plug in the correct direction, the other plug was placed in the empty hole during training trials. Initially, demonstrators were prevented by brackets from removing the other plug. As training progressed, the use of brackets became unnecessary, and both compartments in the plastic box could be filled with mealworms. Training continued until each bird had made 10 correct responses in 5 min, during each of two consecutive training sessions. This criterion was reached after an average of 12 training sessions. Four birds (one red up, one red down and two black up) were excluded from the experiment because they failed to achieve the criterion level of performance after 13 training sessions. An additional red up demonstrator died during the course of instrumental training. To account for these missing demonstrators, five birds demonstrated plug removal to two different observers in replications 1 and 2.

Observer training and testing

Equal numbers of birds were allowed to observe a conspecific demonstrator that had been trained to use its beak to remove either the red or the black plug from the food box, by either pulling up on the loop of string inserted through the centre of the plug (groups red up and black up) or pushing down on the centre of the plug (groups red down and black down).

Before being allowed to observe a demonstrator for the first time, each bird received five daily sessions of training. The birds were trained to feed from the plastic box on days 1, 3 and 5, and habituated to the experimental apparatus on days 2 and 4. The procedure for training to feed from the box was the same as that used with the demonstrators. Habituation training consisted of placing a bird in the observation compartment of an experimental chamber for 30 min. During this period, the bird's demonstrator was present in the adjacent test compartment, but the food container was not.

Each observer was allowed to watch seven demonstration sessions, one per day. Prior to the start of a demonstration session, an observer was removed from its home cage and placed in the observation compartment of a chamber. The bird was allowed to habituate to its surroundings for 2 min, at which point a demonstrator was placed in the adjacent compartment. Observers were paired with the same demonstrator throughout the experiment. Both birds were allowed a further 2-min habituation period, and then the food box was uncovered and the demonstration session commenced. Each session lasted until a demonstrator had made 10 correct, rewarded responses or 10 min had elapsed. Once the session had finished, the food box was covered and both birds were removed from their respective compartments.

We tested each observer three times: immediately after the fifth, sixth and seventh demonstration sessions. The demonstrator was removed from the chamber and the wire-mesh partition was slid back to allow the observer to enter the empty test compartment. Once the observer was in place, the food box was uncovered and the test session commenced. Test sessions lasted 10 min. During this period observers were allowed to take one to three mealworms from the plastic box after each plug removal regardless of the plug, and the direction in which it was removed. Not every removal attempted by an observer was successful. In those cases in which the plug was only partially removed, the bird was given 60 s in which to complete the response. If nothing happened during this period the bird was not rewarded and the plug was returned to its correct position.

Training and testing occurred between 0900 and 1500 hours each day. The order in which the groups were run was counterbalanced between replications to control for time of day.

Videotapes of the observers' test sessions were scored by two independent raters blind to the viewed animal's group assignment. The raters agreed about both the object and direction of the observers' responses on 100% of a randomly selected 30% of test sessions. We calculated two different measurements of the observers' test performance: a spatial discrimination ratio and a directional discrimination ratio. Spatial discrimination ratios were calculated for each bird by dividing the number of responses made to the red plug by the total number of responses. Directional discrimination ratios were calculated by dividing the number of up responses by the total number of responses. As a result of the low within-group variability, we used nonparametric tests to analyse the data. In all cases the tests were two-tailed and the chosen level of significance was $\alpha=0.05$.

RESULTS

Demonstrator and observer birds used similar response topographies when removing the plug. While standing on the lid of the box or the floor of the cage, the bird moved its head towards the plug, opening its beak when its head was within a few centimetres of the plug. For an up response, the mandibles were then closed over the loop of string and the bird thrust its head backwards carrying the plug with it. Once the plug had been removed it was dropped to the floor of the cage. For down responses, the bird thrust its open mandibles against the inner lining of the plug causing it to drop down into the box. Up and down responses showed little variation and were always made with open and closed mandibles, respectively.

Demonstrators' Performance

All demonstrators showed perfect discrimination while being observed. They made 10 responses during 189 of the 224 demonstration sessions. During the remaining 35 sessions they made between one and nine responses. Demonstration sessions lasted, on average, 239 s (range 64–600 s).

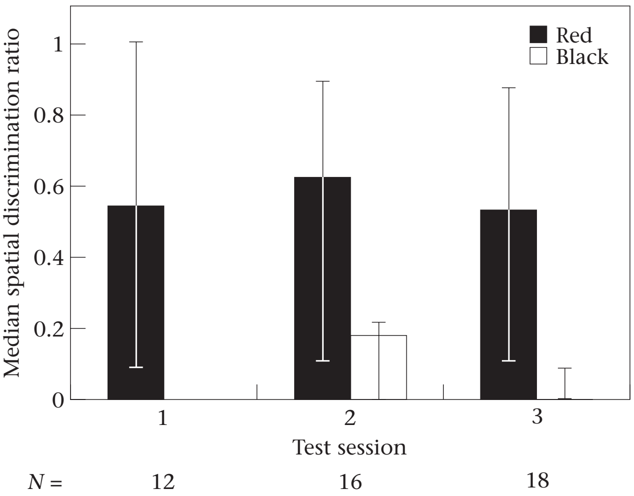

Figure 2. Median spatial discrimination ratio (responses to the red plug/total responses) for the first, second and third test session responses made by birds that observed demonstrators removing either the red or the black plug. Bars show the interquartile range.

Observers' Performance

Of the 32 observers tested, 13 (four red up, one red down, five black up, and four black down observers) failed to respond, that is, to remove a plug during any of the three test sessions, and were therefore excluded from the analysis. Of the 19 that did respond, 11 (three red up, five red down, two black up, and one black down observers) responded on all three test sessions; five (two red up and three black down observers) responded on two test sessions; and three (two red down and one black up observers) responded on one test session. Thus the sample sizes were: red up=5; red down=7; black up=3; black down=4.

Observers of demonstrators trained to remove the red plug made proportionately more of their total responses to the red plug than observers of demonstrators trained to remove the black plug (Fig. 2). However, this effect was significant only during test sessions 1 (Mann–Whitney U test: $U=4$, $N_1=8$, $N_2=4$, $P=0.03$) and 3 (Mann–Whitney U test: $U=10$, $N_1=12$, $N_2=6$, $P=0.01$). During test session 2, the effect was marginal (Mann–Whitney U test: $U=13$, $N_1=10$, $N_2=6$, $P=0.06$).

To determine whether the observers' preference for the plug their demonstrator removed changed over the course of testing, we analysed the data from the 16 birds that responded during two or three test sessions. A Wilcoxon signed-ranks test comparing the observers' spatial discrimination ratios during the first (median 0.17, interquartile range 0.00–0.86) and the last (median 0.13, interquartile range 0.00–0.53) test session on which they responded, indicated no change in the observers' spatial preferences (Wilcoxon signed-ranks

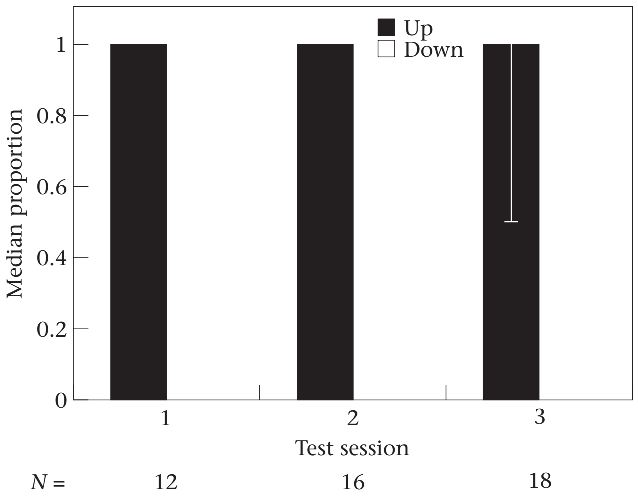

Figure 3. Median directional discrimination ratio (up responses/total responses) for the first, second and third test session responses made by birds that observed demonstrators pulling up or pushing down. Bars show the interquartile range.

test: T=−0.59, N=16, P=0.55). Hence, the data from these birds were pooled across the two or three test sessions on which they responded. Birds that observed demonstrators removing the red plug made proportionately more of their total test session responses to the red plug (median 0.48, interquartile range 0.22–0.77) than birds that observed demonstrators removing the black plug (median 0.09, interquartile range 0.00–0.13; Mann–Whitney U test: U=4.0, N_1=10, N_2=6, P=0.005). However, birds that observed demonstrators pulling the plug up (median 0.46, interquartile range 0.10–0.77) or pushing it down (median 0.16, interquartile range 0.09–0.26) made an equivalent proportion of their total test session responses to the red plug (Mann–Whitney U test: U=23.5, N_1=7, N_2=9, P=0.40).

Observers of demonstrators trained to pull the plug up made proportionately more up responses than observers of demonstrators trained to push the plug down (Fig. 3). This effect was reliable during test sessions 1 (Mann-Whitney U test: U=3.5, N_1=5, N_2=7, P=0.006), 2 (Mann–Whitney U test: U=4.5, N_1=7, N_2=9, P=0.007) and 3 (Mann–Whitney U test: U=10, N_1=8, N_2=10, P=0.001).

A Wilcoxon signed-ranks test was used to analyse the directional discrimination ratios of the first (median 0.00, interquartile range 0.00–1.00) and the last (median 0.00, interquartile range 0.00–1.00) test session responses made by the 16 birds that responded on two or three test sessions. This revealed that the observers' preference for the direction in which their demonstrator responded did not change over the course of testing (Wilcoxon signed-ranks test: T=0.00, N=16, P=1.00). Furthermore, birds that observed demonstrators pulling up made proportionately more of their total test session responses by pulling up (median 1.00, interquartile range 1.00–1.00) than birds that observed demonstrators pushing down (median 0.00, interquartle range 0.00–0.00; Mann–Whitney U test: U=4.5, N_1=7, N_2=9, P=0.0007). However, birds that observed demonstrators removing either the red (median 0.50, interquartile range 0.00–1.00) or the black plug (median 0.00, interquartile range 0.00–0.00) made an equivalent proportion of up responses (Mann–Whitney U test: U=20, N_1=10, N_2=6, P=0.20).

DISCUSSION

Juvenile starlings were influenced by both the object and the direction of a conspecific demonstrator's responses. Birds that observed a demonstrator removing one of two distinctively coloured objects from a hole in the lid of a plastic box by pulling up or pushing down removed the same object in the same direction as their demonstrator.

Observer birds' preference for the object manipulated by a demonstrator provides strong evidence of stimulus learning by observation. This effect could not have been due to social facilitation (Zajonc 1965; Clayton 1978), since observers of red and black demonstrators were exposed equally to the mere presence, general activity and consummatory behaviour of a conspecific. Stimulus learning by observation akin to that found here has been reported by Coleman & Mellgren (1997). They found that zebra finches, *Taeniopygia guttata*, preferred to feed from the same location as a conspecific, while Turner (1969) reported that newly hatched domestic chicks, *Gallus gallus domesticus*, pecked preferentially at grain sharing stimulus characteristics with the grain at which a mechanical model hen was pecking. Furthermore, such effects have been found to persist for many hours after a bird has observed the feeding behaviour of a conspecific (e.g. McQuoid & Galef 1992).

These effects may be examples of either local or stimulus enhancement or observational conditioning. To distinguish between these possibilities it would be necessary to vary or abolish the contingency between the demonstrators' responses and reinforcement. Palameta & Lefebvre (1985), for example, allowed naïve pigeons to observe a demonstrator either piercing a hole in the paper lid covering a food bowl and eating from within, or only eating from a hole in the lid but not piercing it. When subsequently allowed access to the food-finding problem, observers of piercing and eating demonstrators pierced the paper covering an intact food bowl and ate from within, whereas observers of eating but not piercing demonstrators did not. This suggests that the observers that solved the food-finding problem were not simply attracted to the site of their demonstrators' behaviour (local or stimulus enhancement). Rather, they appear to have learned, as a consequence of their demonstrators' behaviour, about a relationship between the paper-covered bowl and food reward (observational conditioning).

The design of our experiment does not allow us to determine whether the observers learned either the location or the colour of the object their demonstrator manipulated, because these two factors were not varied independently. To determine whether location was sufficient to enable observers to learn about the plug their demonstrator removed, it would be necessary to repeat the experiment using two plugs of the same colour. Alternatively, the relative contribution of colour and location could be assessed by testing half of the observers with the plugs in the same position as they had been during observation (group same), and testing the other half with the plugs in the opposite position to which they had been during observation (group different). If the observers learned the location and the colour of the plug their demonstrator removed, then both groups would be expected to remove the same coloured plug as their demonstrator, although this tendency should be stronger in group same than in group different.

Observer birds in our experiment also moved the plug in the same direction as their demonstrator. Such an effect could not have been due to local enhancement, because the demonstrators were not present at the time of testing and it is unclear what residues (e.g. odour cues, food particles) they could have deposited that would have influenced the direction of the observers' responses. Stimulus enhancement is also an unlikely explanation of this effect, since this term is usually reserved for those instances in which a demonstrator's activity renders attractive the object with which the demonstrator was observed interacting, and in our experiment observers of up and down responses saw demonstrators responding at an equal rate to the same object. However, it is possible that the up-lifting and down-pushing demonstrators in our experiment rendered different regions of the plug attractive.

Lefebvre et al. (1997) were faced with a similar problem in their study of Carib grackles, *Quiscalus lugubris*. In this experiment, naïve grackles observed a conspecific or a Zenaida dove *Zenaida aurita*, demonstrator using its beak to remove a plug from an opaque inverted test-tube containing food. To open the tube, grackle demonstrators used an open beak to probe and pull a horizontal stick that protruded from the base of the plug, while dove demonstrators pecked with a closed beak. Lefebvre et al. found that grackles that observed a conspecific demonstrator were more likely to use an open beak to remove the plug than grackles that observed dove demonstrators. These results were interpreted as providing evidence of imitative learning in grackles. However, the two types of demonstrator used in this study manipulated different regions of the stick. Grackle demonstrators probed and pulled the tip of the stick, while dove demonstrators pecked its base. Hence stimulus enhancement rather than imitation might have been responsible for the observers' response bias. Although Lefebvre et al. were able to show that there was no effect of tutor type upon where the observers directed their responses, the only way to exclude stimulus enhancement would have been to train demonstrators to manipulate the same region of the stick.

Finally, the results of a study in which observational discrimination learning occurred in the absence of a conspecific demonstrator (Denny et al. 1988) raises the possibility that the observers in our study may have learned about movement of the plug (emulation learning) or a movement–food relationship (observational conditioning). To investigate this possibility, it would be necessary to perform an experiment in which naïve birds observed a plug moving automatically either up or down in the presence of a conspecific that was simply feeding from the hole whenever the plug was removed. If the birds in our study learned about the direction of their demonstrator's responses, then one would not expect birds exposed to automatic plug movement to show an observation-consistent response bias. If, on the other hand, the birds in our study learned about movement of the plug, then one would expect birds that observed the plug being moved up automatically to make more up responses than birds that observed the plug being moved down automatically.

If the putative response learning effect reported in our experiment, and by Zentall et al. (1996) using pigeons, Akins & Zentall (1996) using quail, and Lefebvre et al. (1997) using grackles, is supported, then the underlying mechanism might have been one of two types. Observer birds may have learned about either a response or a response–food relationship. The former mechanism may be most appropriately described as an example of imitation, and the latter as an instance of observational learning (Heyes 1994). To distinguish between these two mechanisms it would be necessary to perform an experiment in which the relationship between the demonstrators' responses and food reward was varied (e.g. Heyes et al. 1994; Akins & Zentall, in press).

Our results suggest that the two-object/two-action test is well suited for the task of investigating hypotheses about both the distinctive psychological mechanisms and adaptive functions of response learning by observation and stimulus learning by observation, imitative and nonimitative social learning.

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