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A test of imitative learning in starlings using a two-action method with an enhanced ghost control

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Imitative learning, in which an individual learns to reproduce the behaviour pattern of another, has attracted considerable attention as a potentially powerful form of social learning. Despite extensive research, however, it has proved difficult to demonstrate in nonhuman animals. We investigated the ability of European starlings, *Sturnus vulgaris*, to imitate the behaviour of a conspecific. Subjects watched a trained conspecific manipulating a plug for access to a food reward, using either a pushing or a pulling action. When later tested with the same apparatus these birds completed the task using the same action they had previously observed. In a second experiment, a separate group of starlings saw the plug move upwards or downwards automatically and a nearby conspecific obtain a food reward. When given access to the task these starlings failed to move the plug in the direction they had seen. Our experiment is an improvement on previous bidirectional control designs and provides strong evidence that starlings are capable of imitation. We advocate further use of this experimental design in attempts to demonstrate imitative learning.

Social learning refers to any form of learning that occurs through 'observation of, or interaction with, another animal (typically a conspecific) or its products' (Heyes 1994). Under many circumstances such learning will be an adaptive alternative to asocial trial-and-error learning, which may be time consuming or hazardous. Of all the processes thought to result in social learning (Galef 1988; Whiten & Ham 1992; Zentall 1996), that which has received by far the most attention is observational learning or imitation, defined by Heyes (1994) as 'the acquisition of a topographically novel response through observation of a demonstrator making that response'. Many researchers believe this necessitates more complex or sophisticated mental processing than other forms of learning, and some even argue it involves some form of intentionality (Bruner 1972; Tomasello & Call 1997) or theory of mind (Whiten & Byrne 1991). Such claims are hotly disputed (e.g. Heyes 1994; Zentall 1996) but have probably fuelled interest in the subject. Nevertheless, despite over a century of research, imitative learning has been notoriously difficult to demonstrate and only a handful of experiments provide unequivocal support.

Investigations of imitative learning typically expose a naïve 'observer' animal to a task being performed by a trained 'demonstrator' animal, and subsequently test the observer in isolation to see if it has acquired the same behaviour. Such experiments have been plagued by the difficulty of excluding other explanations for a match between demonstrator and observer behaviour. These include local enhancement (Thorpe 1956) and stimulus enhancement (Spence 1937), which involve one animal drawing another's attention to a particular location or type of stimulus in the environment; observational conditioning (Cook et al. 1985), which involves the socially mediated acquisition of a Pavlovian association between a stimulus and a reinforcer (Zentall 1996); and contagion or social facilitation (Zajonc 1965), which occurs when the mere presence of a conspecific influences another animal's behaviour (Zentall 1996), for example by releasing a similar behaviour pattern in that animal.

A significant advance in the study of imitative learning occurred with the development of the two-action/one-outcome method. In this experimental approach the task in question can be completed in two or more distinct ways. Dawson & Foss (1965), for example, trained budgerigars, *Melopsittacus undulatus*, to remove a lid from a cup using either their beak or their foot. When naïve

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budgerigars were allowed to observe one of these techniques they showed a significant tendency to use the same method as their demonstrator. Unfortunately, the paucity of detail in Dawson & Foss's description of their training methods makes it difficult to assess this evidence objectively.

The two-action/one-outcome paradigm has been used successfully to show evidence of imitative learning in pigeons, *Columba livia* (Zentall et al. 1996; Kaiser et al. 1997; but see Campbell et al. 1999), Japanese quail, *Coturnix coturnix japonica* (Akins & Zentall 1996, 1998), and common marmosets, *Callithrix jacchus* (Voelkl & Huber 2000). Critics have found flaws in this technique, however, with Byrne (1994) suggesting that demonstrator-consistent responding could be explained by a combination of stimulus enhancement and 'response facilitation', something similar to social facilitation. If the behaviour to be copied is already in the observer's repertoire, the sight of a conspecific performing that act on a particular stimulus could release the same behaviour in the observer and simultaneously cause it to approach the stimulus. For this reason Byrne (1994) and others (e.g. Zentall 1996) have argued that only copying of a novel action can provide evidence for imitation. However, truly 'novel' behaviour may be hard if not impossible to identify (Heyes 1995), and in practical terms it can be difficult and time consuming to train demonstrators to perform an action that is not already part of their behavioural repertoire.

As an alternative, several researchers (e.g. Collins 1988; Heyes & Dawson 1990; Bugnyar & Huber 1997) have used a variant of the two-action method known as the bidirectional control, in which the two types of demonstrators move the apparatus in different directions for access to a food reward. A tendency of observers to respond in the same direction as their demonstrator is not in itself conclusive evidence of imitation; to rule out other processes, the bidirectional control is typically combined with a 'transfer test' or a 'ghost control'. In a transfer test, the orientation of the apparatus is altered between observation and test sessions. Heyes et al. (1992) used this in an attempt to demonstrate imitation in rats, *Rattus norvegicus*, but it has since emerged (Mitchell et al. 1999; Campbell & Heyes 2002) that odour cues deposited on one side of the manipulandum were guiding the rats' responses. In a ghost control, the manipulandum remains in its original position but is moved automatically without influence from the demonstrator. This reveals whether the demonstrator's behaviour is essential to the learning process, since failure to complete the task under the ghost condition suggests that learning about the movement of the apparatus relative to its surroundings is not, by itself, sufficient. Heyes et al. (1994) used a ghost control in another experiment on rats, but the demonstrator was attending to the food tray and not to the manipulandum when being observed and so local enhancement effects present in the original experiment might also have been excluded from the ghost control (Byrne & Tomasello 1995).

The design of a ghost control can be improved by ensuring that the demonstrator is still present and near the manipulandum when the remote-controlled movement occurs. With this method, which we call an 'enhanced' ghost control, the procedure is as close as possible to the original experiment, with the major exception that the demonstrator's behaviour is not the cause of the manipulandum's movement. Thus although the demonstrator does not make contact with the manipulandum, most of the effects of social facilitation or local/stimulus enhancement will also be present in the control situation.

We attempted to demonstrate imitative learning in European starlings, *sturnus vulgaris*, using a bidirectional control. Our investigation builds on an earlier experiment by Campbell et al. (1999), in which demonstrator starlings were trained to use their beak to push or pull one of two differently coloured plugs for access to a food reward. Campbell et al. found statistically significant levels of response matching in observer starlings, but as the authors admitted this could have been due to stimulus enhancement since the two types of demonstrator manipulated visibly different parts of the apparatus. Furthermore, the absence of a ghost control makes it impossible to distinguish imitative learning from other processes. The observer starlings may have learnt merely about the movement of the plug, either downwards if pushed or upwards if pulled. If they associated this particular direction of movement with the food reward, the observers could have acquired the same response through a process involving stimulus-reinforcer conditioning.

In our experiment, observer starlings were allowed to watch trained demonstrators performing one of the two actions (push or pull) as in Campbell et al.'s (1999) study, but on the same part of the plug. We predicted that, if the observers were capable of imitative learning in this context, they would use the same action as their respective demonstrators when given access to the task. In a follow-up experiment, we used an enhanced ghost control to determine whether the observers' behaviour could have been acquired by processes other than imitation. In this experiment the demonstrator attended closely to the plug but was not responsible for its movement. Under these conditions most of the effects of local or stimulus enhancement were still present, but the remote-controlled movement of the manipulandum precluded any opportunity for imitative learning of demonstrator behaviour by the observers.

EXPERIMENT 1

Methods

Subjects

We used 48 starlings, 12 as demonstrators and 36 as observers. All the birds were caught as juveniles on a farm near Somerton, southwest England. By the start of demonstrator training they had been in captivity for at least 3 months. Those to be used in the experiment were taken from the main starling aviary at the University of Bristol and transferred to wire-mesh cages (120 × 66 cm and 37 cm high) in a nearby room within the animal house.

All training procedures and experiments were conducted in this room. The birds were kept in groups of six to eight.

Fourteen starlings from the main aviary were initially trained as demonstrators. Seven of these had previously been trained in Campbell's et al. (1999) experiment to push or pull one of two plugs for a food reward. The remaining seven had been used as observers in the same experiment. To facilitate the training of these birds, former Push observers and demonstrators were trained as Push demonstrators, and former Pull observers and demonstrators were trained as Pull demonstrators. Owing to poor progress in the training procedure, four of these birds were replaced 1 month after the start of training. The replacements had also been used as demonstrators in Campbell et al.'s experiment and were retrained in their former role.

Following demonstrator training, 36 starlings from the main aviary were prepared as observers. Twenty-four of these were naïve, in that they had not been used in any previous experiments. The remaining 12 had been trained to jump on to a perch for a food reward but were unlikely to have gained any experience that could have biased our experiment.

The experimental room was initially set to a 16:8 h light:dark cycle. Twice during the experiment this was realigned with the changing daylength outside, first by altering it to 12:12 and later to 9:15 h. Light was provided by two computer-controlled 58-W 'natural light' fluorescent tubes. Owing to a failure of the computer control system, two 75/85-W 'truelite' fluorescent tubes were introduced to the room midway through the experiment. Food (in the form of a commercial high-protein chick crumb) and water were provided ad libitum, except when birds were being used in experimental trials or being food deprived prior to this. At about weekly intervals the birds were given mealworms and access to water for bathing.

Apparatus

Training and testing took place in an 18-mm-gauge wire-mesh cage measuring 60 × 66 cm and 37 cm high. For the later stages of training this was divided by a wire-mesh partition into a 'demonstration' compartment and an 'observation' compartment, each measuring 30 × 66 cm and 37 cm high (Fig. 1). A wooden perch was fixed to the front and back walls of each compartment 10 cm from the floor, and a door in the front wall allowed objects to be moved into and out of the cage.

The apparatus for the task, modified from that used by Campbell et al. (1999), consisted of a transparent plastic lunchbox (160 × 107 mm and 55 mm high) and lid (Fig. 2). A sheet of thin white card was glued to the top of the lid and a sponge cloth 10 mm thick was glued to the underside, then a circular hole 38 mm in diameter was cut through all three layers. The hole was positioned closer to one end of the box so that when performing the task a demonstrator could stand on the lid without obstructing the observer's view.

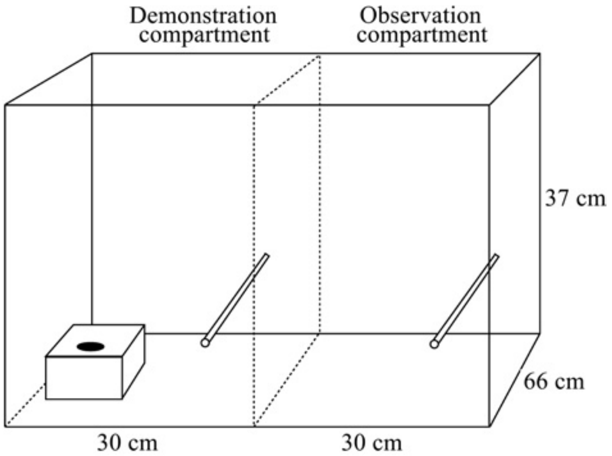

Figure 1. Diagram of the apparatus used for training and testing the starlings. A wire-mesh partition (dotted lines) divided the cage into a 'demonstration' compartment and an 'observation' compartment. The food box, with a plugged hole (filled circle) at one end, was placed in the demonstration compartment.

The plug to be pushed or pulled by the subjects consisted of a blue plastic bottle-top 34 mm in diameter and 13 mm deep. This was turned upside down and used to block the hole in the lid, where it fitted snugly and was held in place by the sponge lining. In this position it acted as a plug which could be pushed into or pulled out of the lunchbox to gain access to a food reward inside.

In Campbell et al.'s (1999) experiment, part of a ping-pong ball was fitted to the inside of the bottle top and a loop of string was threaded through its centre. The Pull demonstrators were trained to grasp this loop of string in their beak to pluck the plug out of the hole, whereas the Push demonstrators pecked in a downwards direction anywhere on the plug to push it into the box, sometimes not making any contact with the string (F. Campbell, personal communication). To ensure that the demonstrators in our experiment attended to the same part of the plug, we removed the string and replaced the piece of ping-pong ball with a small disc of pink sponge. Once attached, the sponge was sliced up with a craft knife to roughen the surface, making it easier for the subjects to grasp with the tip of the beak.

Mealworms, larvae of the beetle *Tenebrio molitor*, were used as a food reward. When given a choice between chick crumb and mealworms, starlings clearly prefer the latter (personal observation). For training and test sessions, mealworms were added to the box so that they covered the bottom.

To aid training of the demonstrators, we fixed metal brackets to the apparatus according to Campbell et al. (1999) so that the plug could be moved in only one direction. Thus, during their period of training, the Pull demonstrators could move the plug only in an upward direction, whereas the Push demonstrators could move it only downwards. During demonstrations to observer starlings, however, the brackets were detached so that movement in either direction was possible.

Procedure

All training and testing took place between 0830 and 1930 hours and on most days was finished by 1700. Prior to its use in a training session or test, each bird was deprived of food for 90–150 min to enhance motivation

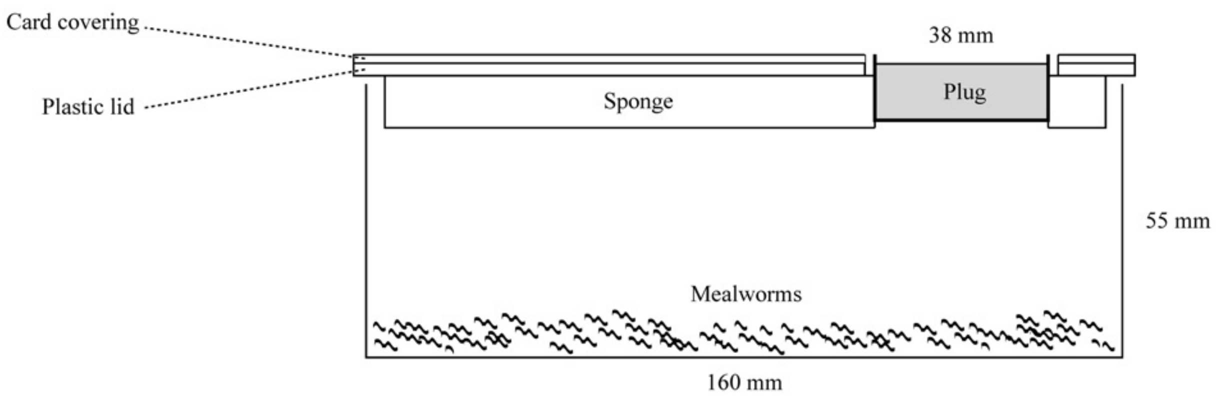

Figure 2. Cross-section of the food box used for training and testing the starlings. The plug was held in position by a piece of sponge cloth glued to the underside of the lid, and could be pushed into or pulled out of the box to gain access to the mealworms inside.

to forage. This is considerably shorter than the food deprivation periods used in similar published studies (e.g. 23 h in Akins & Zentall's 1996 study of imitation in pigeons), but was found to make the birds sufficiently hungry to feed eagerly for several minutes before becoming satiated.

Demonstrator training. To train demonstrators to perform their allocated task, we used a method of successive approximations, with each step of the shaping procedure resembling more closely the target task. For the first stages, all of the demonstrators (Push and Pull) were trained together. The shaping began with exposure of the birds to an open (i.e. lid-less) box containing mealworms. Once all the subjects were seen to have fed from the box its lid was replaced, leaving an open hole through which they could feed. Mealworms were scattered over the lid to encourage them to investigate the hole.

This was the furthest stage to which all the demonstrators could be trained together. Before the plug could be introduced, Push and Pull trainees had to be separated. For each of the subsequent training stages the birds were trained in pairs of the same demonstrator type, and were allowed to watch each other's training sessions in the hope that this would accelerate learning of the task. In general starlings tend to be less active than normal if totally isolated from conspecifics (personal observation). The two birds were placed in the training cage and separated by a wire-mesh partition; they were then given their training sessions in turn, with the partner being allowed to watch through the wire mesh.

The first individual training session required the subject to feed through an open hole as it had done in the communal training sessions. When this was successfully completed we introduced the plug. For the Pull demonstrators it was placed on top of the lid, well away from the hole. Once the bird was proficient at feeding through the hole, the plug was repositioned so that it rested on the edge of the hole and partly blocked it. In the next step the plug rested lightly in the hole but was not pushed into place, and in the final step it sat fully in the hole, gripped by the sponge lining.

For the Push demonstrators we gradually moved the plug from a position on the bottom of the box, below the hole, to one blocking the hole but pushed almost completely through, and finally to a position sitting fully in the hole.

Training sessions lasted for 30 min. A bird would be given no more than two training sessions per day and would remain at the same stage of training until it had made three successful responses within one session. On each successful response the bird was allowed to take three mealworms, but was then shooed away from the box so that the plug could be replaced. If the bird reached the criterion level within its training session it progressed straight to the next stage.

Throughout the shaping procedure metal brackets were in place to prevent the plug moving in the incorrect direction. The final stage of training required the subjects to respond correctly without the brackets in place. Responses in the incorrect direction were not rewarded, with the bird being shooed away before it could obtain reinforcement.

For the purposes of demonstrating to the observers, the reward for each response was cut to a single mealworm. After 90 min of food deprivation the six most proficient Pull trainees and the six most proficient Push trainees each made at least 20 responses within 5 min. We used these 12 birds in the experiment.

Observer training and testing. To minimize any inhibition of learning due to an aversion to novel objects or situations, it was essential that the observer birds were familiarized with the apparatus and the basic elements of the task. Before they were allowed to watch a performing demonstrator, a series of preliminary training sessions (Table 1) introduced the observers to all aspects of the apparatus and the task except for the plug and its manipulation. Owing to constraints on space and the number of demonstrators, we divided the 36 observers into three groups of 12, with the experiment being run in three separate blocks. The same 12 demonstrators were used in each block.

In the first stage of preliminary training we placed an open box of mealworms in the cage housing all 12 observer trainees. The birds were left for 3 h to allow them to habituate to the presence of the box and get used to feeding from it. This was followed by sessions of

Table 1. Schedule for preliminary training, observational training and testing of observers

Day	Procedure
1	Communal training (All observers given 3 h to feed from open box)
2	Box training I (Single observer given 20 min to feed through open hole) Partner training I (Single observer given 20 min in cage adjacent to demonstrator)
3	Partner training II Box training II
4	Observational training I (Single observer watches demonstrator make 15 reinforced responses) Observational training II
5	Observational training III Observational training IV
6	Observational training V+Test Trial I (Single observer watches demonstrator make 15 reinforced responses and is then allowed access to box for 10 min)
7	Observational training VI+Test Trial II
8	Observational training VII+Test Trial III

'box training' and 'partner training'. In box training, an observer was placed in the demonstration compartment and given 20 min to feed through the open hole of the box. The bird was then returned to its holding cage even if it had failed to feed in this time. For partner training, we randomly assigned each observer to one of the 12 trained demonstrators. After 90–150 min of food deprivation, we placed the observer in the observation compartment and its associated demonstrator in the adjoining demonstration compartment. No food was available to either bird during the 20 min of partner training. The purpose of this session was to familiarize the observer–demonstrator pairs so that they were habituated to each other's presence for the later learning sessions. These observer–demonstrator pairings remained throughout the experiment. The birds were then given a second session of partner training, followed by a second session of box training to ensure they were still feeding reliably from the box.

All observers received the same amount of training prior to the test sessions. Birds failing to feed in the box-training sessions progressed straight into the next training sessions along with the other birds. The design of the training protocol was balanced with respect to observer type, such that the time of training and the average length of food deprivation were the same for Push and Pull observers.

Each observer received four initial sessions of observational training, in which it was allowed to watch the demonstrator performing its task. A training session began with the observer and demonstrator being placed in their respective compartments for a 3-min acclimation period. The box, with the plug fitted in the hole, was then introduced to the demonstration compartment and the demonstrator was allowed to perform its task until it had made 15 reinforced responses or 5 min had elapsed. Both birds were then returned to their cages.

Observer testing took place on the following day, immediately after a fifth session of observational training. After the demonstrator had made its 15 reinforced responses and had been removed from the cage, we pulled the wire screen back to allow the observer access to the box. Removal of the demonstrator took no more than 60 s. The observer then had 10 min to make a response. We recorded its first full response, with the plug being completely removed from the hole, whether or not a mealworm was taken. If it failed to make a response within the 10-min test session, we repeated the procedure (an observation session followed by a 10-min observer test period) on the following day. If it failed a second time to give a result, a third and final test trial took place on the day after that.

We made two modifications to the experimental design after the first block of 12 observers had been tested. First, all observers were brought up to the same level of performance in the box training before the first partner-training session was conducted, with extra box sessions being given to slow learners until all birds were feeding consistently through the hole without the need for encouragement. In addition, since several of the observers in the first block had been slow to respond in the test sessions, we introduced a new phase to follow immediately the partner training. At the end of a partner-training session we removed the demonstrator and placed a box with an open hole in the empty compartment. After a few seconds we slid the wire-mesh partition back to allow the observer through for a 10-min period of feeding. We hoped this extra component of preliminary training would get the observer used to feeding from the box as soon as the partition was slid back. These modifications led to a reduction in the response times of the observers but were unlikely to have biased the responses towards either pushing or pulling.

For the second and third blocks, the test trials were not stopped after the first response. Instead we replaced the plug and recorded all responses up to the end of the 10-min test period. While only the first response gave reliable information on social learning of pushing or pulling behaviour, subsequent responses were interesting because they revealed the modifying effect of individual learning on the socially learnt behaviour.

We used two-tailed statistical tests, including a Fisher's exact test to assess whether the responses of the observers were independent of those of their demonstrators. (A chi-square test could not be used because one or more of the expected counts was less than 5.)

Ethical note

The period of food deprivation (90–150 min) we used is within the temporary unavailability of food experienced periodically by starlings in the wild, for example during periods of bad weather. The birds' fat deposits and general body condition were unaffected throughout the study. The experimental protocol was approved by Bristol university. At the end of the experiment, the birds were

Table 2. First responses of observer starlings exposed to a demonstrator that either pushed or pulled a plug for a food reward

	Observer's response	
Demonstrator's action	Pushed	Pulled
Push	15	1
Pull	7	7

transferred to an outdoor aviary (ca. 3 × 6 m and 2.5 m high) to allow them to reacclimatize to outdoor conditions and to gain exercise, especially in flight. After 2–4 weeks they were inspected by the University Veterinary Officer and approved for release back into the wild, in an area regularly occupied by free-living starlings. Body mass and general condition remained stable throughout their time in captivity, being comparable to that of wild conspecifics. The birds used in experiment 2 were treated the same way.

Results

The demonstrators always used the appropriate action, never making an 'incorrect' response, although there was some variation in performance. Out of 144 initial observation sessions (observational training I–IV), the demonstrator made the required 15 responses in 128 of them. Three demonstrators (one Push and two Pull) failed to make their 15 responses in every session. One of these made 15 responses in four of its sessions and averaged 8.43 in the rest; another also made 15 in four of its sessions, averaging 7.00 in the rest; and the third made 14 in one session and 15 in all the rest. In the 52 observation sessions immediately before testing (observational training V–VII), 15 responses were made by the demonstrator in all but five; the number of responses in these five sessions were 11, 14, 14, 5 and 14.

Six of the 36 observers, two Push and four Pull, failed to give a response. For those that did respond (Table 2) there was a significant tendency for the observer to use the same action as its demonstrator (Fisher's exact test: $N=30$, $P=0.012$). Overall there was a stronger tendency to push the plug rather than pull it, but the likelihood of pulling was considerably greater if the observer had previously watched its demonstrator pulling. Demonstrator proficiency, in terms of the rate at which the 15 responses were made, did not predict latency to the observer's first response (Spearman rank correlation: $r_s = -0.077$, $N=12$, $P=0.812$). Latency to the first response did not differ between observers that matched their demonstrator's action and those that did not (Mann–Whitney U test: $U=66.5$, $N_1=8$, $N_2=22$, $P=0.325$), nor between observers that pushed and those that pulled ($U=83.0$, $N_1=8$, $N_2=22$, $P=0.833$).

The push and pull responses involved two distinct uses of the body (Fig. 3). Push demonstrators used a widely gaping beak to effect movement of the plug, resting one mandible on the lip of the hole and pushing down on the plug with the other. Pull demonstrators opened their beak just enough to grab hold of the sponge, then closed it to lift the plug out of the hole. The observers showing the same type of response as their demonstrator did so using a similar technique. Two of the Pull observers that responded with a push initially gripped the sponge between their mandibles and appeared to be trying to pull the plug out, but were unable to do so because the edge of the plug was apparently caught on the lip of the hole. These birds then resorted to pushing with an open beak.

In the second and third runs of the experiment we recorded the observers' responses over a 10-min test period. By the end of the 10 min, six observers had altered their response from a pull to a push, such that only two of the 24 responding observers were still pulling the plug (binomial test: $N=24$, $P<0.0001$).

Discussion

On the face of it this would appear to be good evidence for imitation in starlings. Despite a greater proportion overall pushing the plug into the box rather than pulling it out, observers showed a significant tendency to use the same method as their demonstrators, in accordance with the results of Campbell et al. (1999). More than that, our experiment offers stronger support for imitation than Campbell et al.'s study since it is less susceptible to alternative explanations. In Campbell et al.'s experiment, only the Pull demonstrators grasped the loop of string in their beaks to remove the plug, so it is possible that stimulus enhancement could have contributed to the difference in responses of the two groups of observers. The present experiment, in contrast, ensured that both Push and Pull demonstrators made contact with the same part of the manipulandum.

The high number of Push responses leads us to suspect that pushing is a more natural response for the starlings than pulling. Such a bias towards pushing would not be surprising given the usual mode of feeding in the starling's natural environment (Feare 1984). When feeding on grassland the birds probe the turf in search of invertebrates, opening their mandibles as they push downwards to create a channel for viewing prey. The seven Pull observers in our experiment that pushed the plug may have done so through a combination of local enhancement and an increased motivation to forage from seeing their demonstrator feed; they were attracted to the plug and were stimulated to investigate it using their normal foraging technique. If we assume a similar 'background' level of pushing in the Push group, with half (eight) of the responding observers doing so by non-imitative means, then of the remaining 15 observers (from both groups) all but one matched the action of its demonstrator. However, this interpretation of pushing as a more 'natural' response must remain entirely speculative in the absence of a 'baseline' control group, in which starlings who have not seen demonstrators are exposed to the same task.

Six of the eight observers that initially responded with a pull changed to a pushing response over the 10-min test session. This contrasts with the results of Campbell et al.

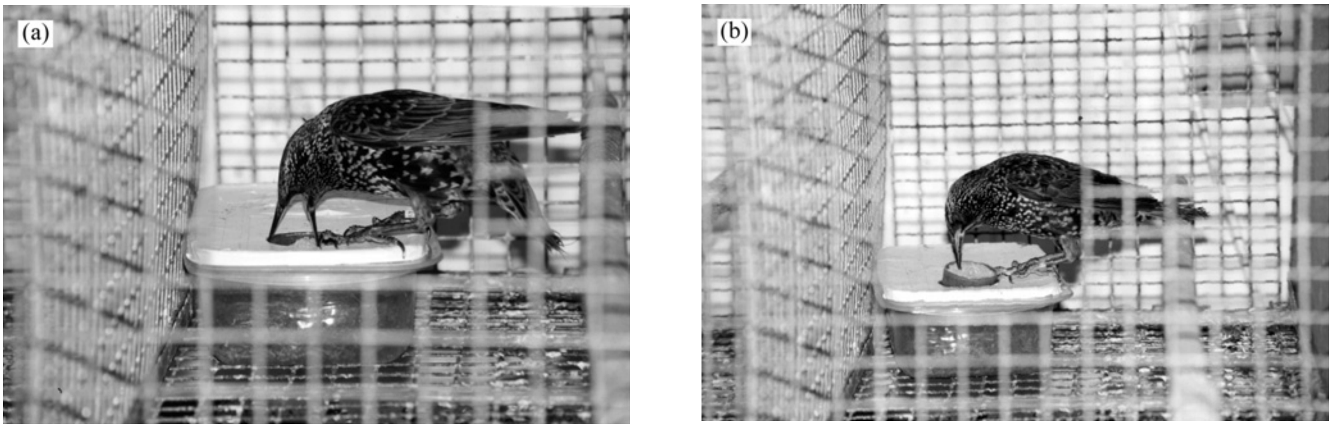

Figure 3. Typical response topographies of (a) a Push demonstrator and (b) a Pull demonstrator. Note the widely gaping beak of the Push demonstrator.

(1999), who reported high levels of demonstrator-consistent responding in Pull as well as Push observers, and that the preference for these actions remained stable over three test sessions. Differences between the apparatus used in the two experiments could be responsible for this discrepancy. In Campbell et al.'s study, both types of response required contact with a particular part of the manipulandum for which it would be difficult to make the opposite response (i.e. the subjects could not use the loop of string to push, and there was nothing on the main body of the plug they could pull on). In the present experiment both Pull and Push observers made contact with the same part of the plug when responding, which may have increased the chances that they would make an 'incorrect' response. In particular, when the Pull observers tried to grasp the sponge to pull the plug out, it might have been easy inadvertently to push it in.

The most proficient demonstrators did not produce the most quickly responding observers. Perhaps this is not surprising, since demonstrators that respond at a very fast rate might be difficult to learn from. This interpretation is consistent with the results of Vanayan et al. (1985), who found that the observers in their experiment learnt more easily from poor demonstrators.

EXPERIMENT 2

Despite the promising results, experiment 1 does not conclusively demonstrate imitation. An alternative explanation is that the observers were learning not about the behaviour of the demonstrator, but rather about the movement of the plug in relation to its surroundings; that is, whether the plug moved into or out of the box, downwards or upwards. To discriminate between these conflicting hypotheses we conducted a second experiment. This used an enhanced ghost control, constructed in the same way as the original experiment with the exception that the behaviour of the demonstrator did not effect movement of the plug. We predicted that, if the response matching in the first experiment was due to learning about the movement of the plug, it would also be seen in the ghost control. If, on the other hand, the observers had truly imitated the behaviour of their demonstrators, they would not be able to do so in the control and response matching would not be seen.

Methods

Subjects

We used 24 observers, divided into two runs of 12. All of these birds had previously been trained in a separate experiment to associate a light stimulus with presentation of food, something of little relevance to the present investigation. The lighting was kept on a 9:15 h light:dark cycle and food and water were available ad libitum when the birds were not in use. The same 12 demonstrators were used as in experiment 1, but owing to poor performance one of these had to be dropped. To replace it, one of the remaining demonstrators was used twice in each run of the experiment.

Apparatus

The basic apparatus was unchanged from experiment 1 but we could move the plug remotely with a length of thin monofilament fishing line attached to its centre. For the Push demonstrators, the fishing line was threaded through a pinhole in the bottom of the box directly below the plughole, so that when tugged it caused the plug to be pulled downwards out of the hole. For the Pull demonstrators, the line was looped over one of the bars in the roof of the compartment, so that a short tug on the end of the line lifted the plug out of the box. For observer testing we used a normal plug without the fishing-line attachment.

Procedure

Observers were trained according to the procedure used in experiment 1, with the exception that the demonstrators were not responsible for making the plug move. In observational training each demonstrator was allowed to make 15 responses as before, but this time the plug was pulled into or out of (depending on demonstrator type) the hole by remote control before the demonstrator was

Table 3. First responses of observer starlings exposed to a ghost control in which a plug moved either into ('Push') or out of ('Pull') a food box attended to by a demonstrator

	Observer's response	
Remote-controlled movement	Pushed	Pulled
Push	9	0
Pull	4	1

able to make contact with it. For both Push and Pull groups the demonstrator was required to approach the box and stand on top of the lid before the plug was removed. We allowed it to take one mealworm as reinforcement and then replaced the plug by hand as in experiment 1. Great care was taken to ensure that the demonstrator made no contact with the plug in any of the sessions where an observer was present.

Apart from the remote control of the plug, observers were exposed to a situation almost identical to that in experiment 1. In the test sessions we replaced the plug with an unmodified one (without fishing-line attachment) before allowing the observer through to the demonstration compartment. All responses over a 10-min period were noted and subsequent test trials, up to a maximum of three, were given if no response had been made.

Results

Of the 24 observers, 16 made at least one response. Two of these were excluded from the analysis because of the nature of their responses: one stepped on the plug and in doing so pushed it into the box, while the other prised it out with its beak. The remaining 14 birds made responses that were clearly either a push or a pull, and it is on these results (Table 3) that the analysis is based.

Unlike in the original experiment the observers showed no tendency to copy the action they had seen (Fisher's exact test: N=14, P=0.357), with 13 out of 14 pushing the plug. This differs from the results of the previous experiment, where observers significantly matched their demonstrator's action. The one bird that initially pulled the plug had switched to pushing by the end of the 10-min test period, emphasizing the strong tendency of the starlings to use the push action.

GENERAL DISCUSSION

The results of experiment 1 show clearly that the observer starlings learnt to respond in the same way as their demonstrators. On their own, however, the results do not reveal the mechanism of learning and hence do not prove that imitation occurred. In the enhanced ghost control (experiment 2), where the procedure was almost identical but lacked the critical plug-manipulating behaviour of the demonstrator, observers failed to learn as they had done in the original experiment. Instead, all but one of the responding birds pushed the plug. This lack of behavioural matching suggests that observation of the demonstrator's behaviour was a crucial component in acquisition of the response, and that the observers were not simply paying attention to the movement of the plug. Our results provide the first strong evidence of imitation in starlings.

Putting these results alongside those of Zentall et al. (1996) and Akins & Zentall (1996, 1998), there is now good evidence for imitation in three avian orders. If the capacity to imitate requires a certain level of cognitive sophistication, it would seem that this level of sophistication is not restricted to primates, and the phenomenon may be much more widespread than was once thought. On the basis of current evidence, birds have emerged as good subjects for investigations of imitative learning, and perhaps avoid some of the additional complications of experiments involving primates (Heyes & Ray 2000).

For a number of reasons the ability to learn about another's foraging activities may be beneficial to birds that feed or roost in flocks (Galef & Giraldeau 2001). A bird could potentially increase its foraging efficiency by following knowledgeable conspecifics to new patches of food, by expanding its diet to include novel food types it has seen conspecifics eating, or by acquiring behavioural techniques shown by conspecifics to take advantage of otherwise inaccessible foods. Of course, the exchange of information in this way may also carry costs for the knowledgeable individuals in the form of increased competition for resources.

Such benefits and costs are particularly apparent in the case of scrub jays, *Aphelocoma coerulescens*. In this species, individuals profit directly from the foraging of others by pilfering the food they have cached (Clayton & Dickinson 1998). In a recent study, Emery & Clayton (2001) found that jays caching food items in the presence of a conspecific observer will recache these items when the observer is no longer there, thwarting its attempts to steal the food. Evidence on the benefits of social learning from a wide range of other species is also well documented (reviewed by Galef & Giraldeau 2001). Despite this, the adaptive significance of imitation as opposed to simpler processes is poorly understood and warrants further investigation. Some have suggested that imitative learning permits higher copying fidelity for observed actions (e.g. Tomasello 1994), but this has not been shown empirically and it is not clear exactly what the advantages of high-fidelity transmission might be.

Although our results strongly suggest that starlings can imitate, the design of our experiment was by no means perfect. As with other techniques, there are difficulties with using a bidirectional control to demonstrate imitation. This paradigm is commonly presented as its own control, but it is not an ideal control because the different demonstrator response topographies have different effects on the apparatus. Our enhanced ghost control sought to overcome this problem by eliminating the demonstrator's role in manipulating the apparatus, while otherwise keeping the procedure as similar as possible to that in the original experiment. Nevertheless, there were other subtle ways in which the control conditions differed from those in the original experiment, for example the presence of the fishing line, which was potentially visible to the observers in the Pull treatment. It is difficult to see how something like this could have biased the results in any way, but it would have been preferable to use a control in which the apparatus appeared identical to that in the original experiment.

The most compelling evidence for imitation in other birds comes from the two-action/one-outcome experiments of Zentall et al. (1996) and Akins & Zentall (1996, 1998). (Lefebvre et al. 1997 also claimed evidence of imitation in Carib grackles, *Quiscalus lugubris*, using a similar technique, but, as acknowledged by the authors, the two groups of demonstrators made contact with different parts of the manipulandum.) In each of these studies, observer birds watched a demonstrator either pecking or stepping on a treadle for access to a food reward and were later found to use the same response topography when faced with the same task. Even this may not constitute conclusive proof of imitation, however, since it is possible that the observed response matching could have resulted from a combination of response facilitation and local or stimulus enhancement (Kaiser et al. 1997). It could be that pecking demonstrators released in their observers a similar pecking response directed towards the treadle, whereas observers of stepping demonstrators, in the absence of a pecking releaser, could have stepped on the treadle by chance as they wandered around the experimental chamber. Kaiser et al. (1997) attempted to exclude this alternative explanation by showing that observers of demonstrators that did not attend to the treadle made significantly fewer stepping responses. Unfortunately this design also inadvertently excluded any effects of local enhancement, which might have been part of the necessary stimulus for treadle-directed behaviour in observers (Campbell et al. 1999).

The same criticism might be levelled at our experiment, in that our results could be explained by a pecking response being released in the Push observers but not in the Pull observers. However, this cannot account for the seven Pull observers in the original experiment that pulled the plug with their beak, an unusual response and therefore one unlikely to be produced through local enhancement alone. In Zentall et al.'s (1996) experiment, in contrast, the chances of a pigeon inadvertently stepping on a treadle as it wandered around the chamber, particularly when its attention might have been drawn to that treadle by the demonstrator, are likely to have been comparatively high. With our starlings, the one observer response that did appear to be due to chance, with the individual stepping on the plug and pushing it through the hole, was excluded from our analysis.

Published studies of imitative learning and other processes of social learning have typically used one or a few demonstrators. The present experiment represents a substantial improvement in this respect, with 12 demonstrators being used. Although a single demonstrator of each response topography is all that is required to show that imitation can potentially occur, the interpretation of results with low numbers of demonstrators is complicated by the problem of pseudoreplication (Hurlbert 1984). In the extreme case where just one demonstrator is used for each action, response matching in the observers could be attributed to any difference between those two particular demonstrators, which may or may not have anything to do with their trained actions.

Furthermore, using a large number of demonstrators will help to increase statistical power in detecting learning (response matching) effects, since some of the variability in observer performance will reflect the variability in demonstrator performance, and some models might simply be poor ones to learn from. Hence to maximize statistical power it is important to increase the sample size of demonstrators as well as observers. Finally, a large sample of demonstrators allows some assessment of the potential for cultural transmission. Response matching with several different demonstrators suggests that information exchange may be a relatively common process and not restricted to a minority of skilled foragers. This is of obvious ecological interest, since the spread of foraging techniques between many individuals in a social group could dramatically enhance the effectiveness of their foraging (Giraldeau 1984; Giraldeau et al. 1994; Templeton & Giraldeau 1995).

The design of our experiment represents a marked improvement on the bidirectional controls used in previous studies. A bidirectional control on its own is not sufficient to demonstrate imitation; further experiments are needed to elucidate the mechanism of learning involved. We have shown that this can be done using an enhanced ghost control, preserving as much as possible of the opportunities for social facilitation, local and stimulus enhancement and observational conditioning present in the original experiment. We hope that our work will stimulate further research in this area using similar techniques, which constitute a viable alternative to the two-action/one-outcome paradigm for investigations of imitative learning.

Nearly all claims of imitation in the literature have been hotly contested, but the findings of Zentall et al. (1996), Akins & Zentall (1996) and the present experiment suggest strongly that imitation is not unique to humans, apes or even primates. Imitation may be a much more widespread phenomenon than was previously thought, and further experiments are needed to test this. With a knowledge of which animals are able to imitate and which are not, we can begin to understand why these differences exist and how the learning abilities of a species have been influenced by natural selection.

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