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Seeing how it's done: matching conditions for observer rats (*Rattus norvegicus*) in the bidirectional control

Abstract In an attempt to increase the reliability of the demonstrator-consistent responding effect produced in the bidirectional control procedure, experiments 1–4 sought conditions that would magnify the matching effect. The aim was to produce a robust demonstrator-consistent responding effect in order that future analytic experiments could investigate the psychological processes responsible for this effect. The joystick responses of observer rats trained using the standard bidirectional control procedure parameters were compared with those of observers subject to conditions identified in the social learning literature as favourable for imitation. Unlike mice, observer rats in experiments 1 a and 1 b tended to push a joystick in the same direction as their demonstrators when the demonstrators were either familiar or unfamiliar males and females. Comparable demonstrator-consistent responding occurred following observation of a standard and a salient joystick response (experiment 2). Experiment 3 showed that the discriminative accuracy of a demonstrator's responding was important for matching behaviour, and suggested that matching might be enhanced with more than the conventional single observation session. Experiment 4 confirmed that the bidirectional control effect is sensitive to the amount of observational experience; after six observation sessions, demonstrator-inconsistent responding occurs. The results of experiments 1–3 are, and those of experiment 4 are not, compatible with the hypothesis that demonstrator-consistent responding in the bidirectional control is caused by olfactory cues deposited by demonstrators on the joystick.

Key words Social learning · Observational learning · Bidirectional control · Odour cues · Observer rats

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Introduction

Thanks to increasingly sophisticated experimental methodologies, we now have respected (if not conclusive) evidence that primates (including chimpanzees, Custance et al. 1995; and monkeys, Bugnyar and Huber 1997) and birds (Akins and Zentall 1996; Campbell et al. 1998; Lefebvre et al. 1997) can imitate body movements i.e., that they are capable of "motor imitation". In the Custance et al. (1995) study, for example, two laboratory-reared chimpanzees were taught, by rewarding approximate attempts, to reproduce 15 separate modelled actions on the command "Do this". Novel actions were subsequently introduced, and from judgements made by independent raters of video recordings of the chimpanzees' behaviour the authors concluded that each chimpanzee reproduced roughly a third of the new actions. Rigorous methods ensured that reproductions of the novel acts could be said to be imitative. The authors were, for example, careful to deliver necessary motivational rewards independently of the chimpanzees' imitative success on test, and to establish the data's reliability by subjecting the inter-rater agreement to detailed statistical scrutiny.

Evidence of imitation in animals is important because of the special role imitation is thought to play in culture, effecting information transmission between individuals and generations (Boyd and Richerson 1985; Tomasello et al. 1993). From this perspective, promising evidence of motor imitation in birds is somewhat surprising because it suggests that, in addition to primates, taxa that are only very distantly related to humans have the psychological processes necessary for imitation learning. Thus, evidence of imitation in birds raises the possibility that imitative processes are widespread across taxa. However, instead of representing a phylogenetically general capacity for imitation, motor imitation in birds may be related to the capacity for vocal imitation found in many avian species. One way to test the latter hypothesis is to seek evidence of motor imitation in animals that are neither primates nor vocal mimics, for example, in rats. Evidence

of motor imitation in rats would favour the hypothesis that imitation is mediated by a phylogenetically general process, while evidence that rats are incapable of imitation would support the hypothesis that avian and primate imitation have evolved separately, under distinct selection pressures.

From experiments by Heyes and colleagues there is currently some reason to believe that rats can imitate a directional joystick response in a bidirectional control procedure (e.g. Heyes and Dawson 1990; Heyes et al. 1992, 1993, 1994). In these studies, each magazine-trained "observer" rat confronted a conspecific "demonstrator" as the latter pushed a joystick to the observer's left or to the observer's right for food reward. The demonstrator was removed from the operant chamber when it had made 50 reinforced responses, and the observer was given access to the joystick from the position previously occupied by the demonstrator. On test, observers were rewarded for responses in either direction, and they showed a reliable tendency to push the joystick toward the same location in space, and in the same direction relative to the actor's body, as had their demonstrators.

In a further, transfer experiment (Heyes et al. 1992), the joystick was moved to an adjacent wall after observation and before the test. In its new position, the joystick moved in a plane perpendicular to that in which it had moved during observation. Consequently, when an observer pushed the joystick in the same direction relative to the actor's body as its demonstrator, the joystick moved toward a different location in space. Under these conditions, as in the previous experiments, the observer rats showed a reliable tendency to push the joystick in the same direction relative to the actor's body as had their demonstrators.

These results were interpreted as evidence that rats are capable of observational learning, that they can learn a response or a response-reinforcer relationship by observation, and it was anticipated that the bidirectional control procedure could be used for analytic investigation of this type of learning. Subsequent studies have fulfilled this potential to some degree by providing information about the conditions in which demonstrator-consistent responding occurs in this procedure. For example, they have shown that the effect is present among naïve observers when the demonstrators' responses are each followed by a tone and delivery of food to the demonstrator, but not when the demonstrator receives food alone, tone alone, or responds in extinction (Heyes et al. 1994). In addition, experiments using the bidirectional control procedure have indicated that when observers have been pretrained by conventional methods to push the joystick in one direction, exposure to a demonstrator pushing in the same direction without reinforcement (group Same) reduces the observer's resistance to extinction to a greater extent than exposure to a demonstrator responding in the opposite direction without reinforcement (group Different) (Heyes et al. 1993). Both groups Same and Different showed less resistance to extinction than group None which had observed a passive demonstrator. This "observational extinction" effect suggested that rats can learn a response-no reinforcer relationship by observation.

However, in the course of conducting these and other, unpublished experiments, it has become clear that under the exposure and test conditions used in the original experiments (e.g. Heyes and Dawson 1990; Heyes et al. 1992, experiment 1), demonstrator-consistent responding in the bidirectional control procedure is a real, but not a robust, effect. Null results have been obtained in many attempts to replicate the basic effect, and a recent meta-analysis of such attempts estimated that more than 33 observer rats per treatment group would be necessary to detect demonstrator-consistent responding with 80% power across all experiments (Gardner 1997).

A further difficulty with the bidirectional control concerns the role of residual odour on the joystick in promoting demonstrator-consistent responding. A recent bidirectional control experiment (Mitchell et al. 1999) found that observers for whom the joystick had been rotated through 180° in between observation and testing tended to push the joystick in the opposite direction to their demonstrators. The authors explained the influence of joystick orientation on observers' preferred response direction by suggesting that demonstrators deposit odour cues on the joystick when they push it. By predominantly contacting the joystick surface contralateral to their response direction, the demonstrators leave an asymmetric odour cue which is located differently for observers of left and right joystick responses. When the joystick remains unmoved on test, observers of left pushing are attracted to the scent-bearing right-hand side of the joystick, and from there a left response is most likely. When the joystick is rotated, scent cues are relocated to its left-hand surface for these left pushing observers, and attraction to odour facilitates demonstrator-inconsistent responses to the right.

Bidirectional control experiments that could establish odour deposits as a sufficient cause for demonstrator-consistent responding have not been run. We do know, however, that a scent hypothesis cannot explain all of the reported bidirectional control effects. Taking the studies cited earlier, it seems that demonstrator-consistent responding requires observation of a demonstrator that is rewarded for its responses (Heyes et al. 1994), and attraction to scent does not explain effects like observational extinction, in which observers' test performance is improved in the absence of scent cues for direction (Heyes et al. 1993).

The purpose of the experiments reported here was to find conditions which magnified demonstrator-consistent joystick responding by varying the standard bidirectional control procedure parameters. It might reasonably be expected that a stronger behavioural matching effect would prove more reliable, and provide a stronger basis for analytic investigation of processes, olfactory or otherwise, responsible for rats' apparently imitative joystick behaviour. The performance of observers trained using these new parameters was compared with that of animals trained under the conditions of the original bidirectional control experiments (Heyes et al. 1992). The particular variables chosen

for manipulation in these experiments were some of those that the social learning literature identifies as important for matching behaviour.

Humans and certain non-human primates have been shown to imitate certain demonstrators selectively (Bandura 1986; Russon and Galdikas 1995). Therefore, experiments 1 a and 1 b examined whether either familiarity with the demonstrator, or the demonstrator's sex, would affect demonstrator-consistent responding. In response to the interpretation of the bidirectional control procedure offered by Byrne and Tomasello (1995), an attempt was made in experiment 2 to increase the salience of the demonstrator's joystick pushing response. In experiment 3, half the demonstrators made a proportion of their responses in the "wrong", nonreinforced direction, because observation of non-proficient performance has been shown to facilitate observational discrimination learning in pigeons (Vanayan et al. 1985), and observational conditioning in zebra finches (Beauchamp and Kacelnik 1991). The amount of observational exposure was varied in experiment 4. For half the observers, testing followed seven observation sessions of 50 reinforced responses. Previous demonstrator-consistent responding effects in the bidirectional control procedure had been found after observation of 50 reinforced responses, but it was apparent from the literature that matching behaviour was typically demonstrated in comparable procedures following more extensive observational experience (Denny et al. 1988; Collins 1988; Oldfield-Box 1970)

Experiments 1a and 1b

In a recent observational study of the spontaneous imitative behaviour of free-living rehabilitant orangutans, Russon and Galdikas (1995) reported that the likelihood of matching behaviour was affected by the imitator's relationship with the model. For example, parents were the models for many more instances of matching behaviour than "friends". Human subjects have also been shown to be discerning imitators, responding selectively to, for example, a human model's prestige (Bandura 1971), skill (Meltzoff and Moore 1992), or attachment to the observer (McCabe and Uzgiris 1983). By selectively imitating models that are, for example, familiar or skilled, the observer may effectively be selecting "knowledgeable" models, and therefore, unlikely to learn behaviour that is either detrimental to fitness, or irrelevant and costly to acquire (Russon and Galdikas 1995).

Experiments 1a and 1b manipulated the characteristics of the demonstrators in the bidirectional control procedure; they were either familiar or unfamiliar, male or female. In experiment 1a observers and demonstrators were housed separately and encountered one another for the first time during the observation session. In experiment 1b and in previous bidirectional control studies, observer-demonstrator pairs were housed together for several days prior to observation and testing. Half of the subjects in

each experiment observed a demonstrator pushing to the left (group Left) and half to the right (group Right). All of the observers were male, and in experiment 1a, half of the animals in each group observed a male, and half observed a female, demonstrator. Observers in experiment 1a should show less demonstrator-consistent responding if, as in primates, social learning in rats is fostered by familiarity with the model. Investigation of the effect of demonstrator sex was prompted by the report of Collins (1988) that male mice show behavioural matching with female, but not male, demonstrators.

Methods

Experiment 1a

Subjects. Thirty-two hooded Lister rats, obtained from Charles Rivers (UK), served as subjects. Sixteen of these, the observers, were male and approximately 3 months old, and the remainder, the demonstrators, were approximately 6 months old. Half of the demonstrators were male and half were female. The subjects were housed in same-sex groups of four (demonstrators and observers separately) in moulded plastic and metal hanging cages (54 × 32 × 21 cm), with free access to water, and maintained at 85% of their free-feeding body weight throughout the experiment.

Apparatus. The animals were trained and tested in four identical operant chambers, each measuring 50 × 25 × 20 cm. The walls were made of sheet metal, the ceiling of clear Perspex, and the floor was of metal grid construction. Each chamber was divided into two compartments of equal size by a 1-cm-gauge wire-mesh partition. In the compartment used for demonstrations and testing, an aluminium alloy joystick (0.6 cm in diameter) was suspended from the ceiling, half way between the side walls. The free end of the joystick, which was 6.5 cm above the floor when the joystick was in a vertical position, could only be moved to the left or to the right in a plane parallel to that of the partition. The joystick was separated from the partition by a distance of 4 cm. This distance was great enough to prevent an observer rat from reaching through the partition and contacting the joystick during observation, and small enough to prevent an animal in the demonstration/test compartment from manipulating the joystick from the partition side. The latter ensured that when observers were responding on test, they were facing in the opposite direction to that from which they had viewed the joystick during observation training.

Movement of the joystick by the demonstrators and observers was recorded via a low-torque potentiometer pivot at the top of the joystick, above the roof of the chamber containing the animals. A constant voltage was applied across the pivot. Movement of the joystick by a rat resulted in rotation of a brush within the potentiometer, and hence to a voltage proportional to the degree of joystick displacement becoming available at the brush termi-

nal. This DC potential was converted to a digital signal read by a BBC Master computer running Spider on-line control language. When being observed, demonstrators had to displace the free end of the joystick 7.5 cm in order to register a response, and when observers were being tested the necessary displacement was 4 cm. After displacement, the joystick was assisted back to a vertical position by a weight and a spring resting on the pivot of the manipulandum.

In addition to the joystick, the demonstration/test compartment contained a food tray situated at floor level in the middle of the wall opposite the partition. The food tray was illuminated on the inside by a 24-V, 2.8-W bulb, and entries to the tray were recorded via a photocell beam. Whenever a food pellet (45 mg, mixed composition) was delivered to the tray, a 1000-Hz, 90-dB tone of 0.1 s duration sounded simultaneously, the house light went out and the tray light was illuminated. The house light was switched on, and the tray light was switched off, 5 s later, or, if a tray entry was made within 5 s, when the next tray entry was registered.

Procedure. Each session began with illumination of the house light and ended after 50 reinforcers had been delivered when the house light was switched off. A response was scored as "left" if it resulted in a displacement of the joystick towards the front/door side of the operant chamber, and as "right" if it resulted in displacement of the joystick in the opposite direction. As observers and demonstrators faced one another on opposite sides of the partition and of the joystick, when a demonstrator made a "right" response the joystick moved to the left in the demonstrator's visual field and to the right in the observer's visual field.

Demonstrator training. Initially, each of the demonstrators received four daily sessions of magazine training in the demonstration/test compartment from which the joystick had been removed. Thirty food pellets were delivered on a random time 60-s schedule in each session. Half of the animals were then trained to push the joystick to the left and half to push it to the right in ten daily sessions. Of the demonstrators trained to push in each direction, half were male and half were female. In the first session of instrumental training, each joystick displacement of 2.5 cm or more in the appropriate direction was followed by the delivery of a food pellet, provided that a magazine entry had been registered since the delivery of the previous reinforcer. (This magazine requirement was in operation, from the second joystick response onwards, in all instrumental sessions, for observers and demonstrators.) In the second session the criterion displacement was 5 cm, and from the third session onwards it was 7.5 cm. To allow demonstrators to become accustomed to being observed while pushing the joystick, a "dummy observer" was placed in the observation compartment during each demonstrator's final three sessions of training. The dummy rats, which were about the same age, and of the same gender, as the demonstrators, had received in-strumental training in the apparatus as part of a previous experiment.

Observer training and testing. The observers were magazine-trained in the same way as the demonstrators. Before being allowed access to the joystick for the first time, each observer was placed in the observation compartment while a demonstrator pushed the joystick 50 times with continuous reinforcement to the left or to the right. When the demonstrator had made 50 responses, it was removed from the apparatus, and the observer was immediately transferred to the demonstration/test compartment where joystick displacements of 4 cm or more in either direction were reinforced. This test phase ended when the observer had made a total of 50 reinforced responses, or after 1 h.

Experiment 1b

The method used in experiment 1b was identical to that of experiment 1a except that all of the demonstrators were male, and observers and demonstrators were housed together, in cages containing two observer-demonstrator pairs, for 5 days prior to observation and testing.

The subjects were 32 male hooded Lister rats, obtained from Charles Rivers (UK). The 16 observers were approximately 3 months old, the demonstrators were approximately 4 months old.

Results and discussion

All of the demonstrators except one showed perfect discrimination while being observed, and the remaining animal, which demonstrated for a subject in experiment 1a, group Right, made just two incorrect responses.

Two observers in experiment 1a (one in group Left and one in group Right) failed to complete 50 reinforced responses on test and were therefore excluded from the analysis. Thus, the group sizes were: 1a, Left = 7, Right = 7; 1b, Left = 8, Right = 8.

A discrimination ratio was calculated for each of the observers by dividing the number of left responses by the total number of responses made during the test session. The mean discrimination ratio for each group in each experiment is given in Fig. 1. The data from experiment 1a were subjected to analysis of variance in which direction (left or right) and demonstrator sex, were factors. The main effect of direction was significant ($F_{1,10} = 4.17$, $P = 0.033$, one tailed), indicating that, as in previous bidirectional control experiments, observers of left pushing pushed the joystick to the left more than observers of right pushing. This could either be because observers in groups Left *and* Right matched the direction of their demonstrators' responses, or because a single group showed demonstrator-consistent responding. There was no effect of demonstrator sex ($F_{1,10} = 0.7$, $P = 0.4191$) and no interaction between group and sex ($F_{1,10} = 1.71$, $P = 0.22$). One-way analysis of variance on the data from experiment 1b

Fig. 1 Mean discrimination ratios (left responses divided by 50, the total number of test responses) for each group of observers in experiments 1a and 1b. *Bars* indicate SEs
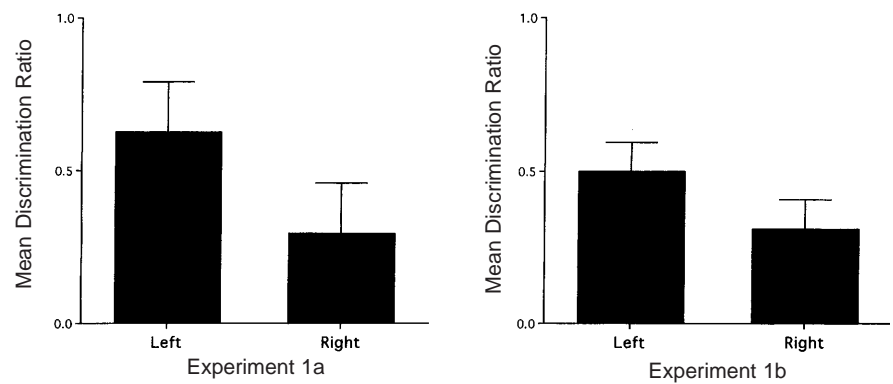
confirmed that the observers of left pushing in that experiment also made a greater proportion of left responses that observers of right pushing ($F_{1,13} = 4.55$, $P = 0.05$).

The results of experiment 1a indicate that, in the bidirectional control procedure, rats show demonstrator-consistent responding when their demonstrators are unfamiliar individuals that they have not encountered prior to the observation session. Furthermore, while cross-experimental comparisons must be made with care, the similarity of the results of experiments 1a and 1b suggests that lack of familiarity with demonstrators does not result in any detectable attenuation of imitation. Finally, it is noteworthy that in experiment 1a there was no indication that unfamiliar males were either more or less effective than unfamiliar females as demonstrators for male rats.

Experiments 1a and 1b provide no evidence that the sex of, or familiarity with, a demonstrator modulate the likelihood of matching behaviour in the bidirectional control. It is not clear how this null result should be interpreted with regard to comparing matching processes in rats and primates because the mechanisms of selectivity in primates are not yet understood. Thus, for example, in the Russon and Galdikas (1995) study, orangutans may have imitated their parents more often than other available models because they spent more time in close proximity to their parents. To the extent that selectivity effects in orangutans are emergent properties of the opportunity for observational experience, a variable which is controlled in the bidirectional control procedure, the demonstrator-consistent behaviour of rats should be insensitive to demonstrator characteristics. In any event, on the basis of the current data, this selectivity variable does not promise to increase the magnitude of demonstrator-consistent responding in the bidirectional control.

Collins (1988) reported a sex difference in demonstrator-consistent responding by mice exposed to a female demonstrator; only male observers matched a directional response. Our failure to demonstrate selective matching on the basis of sex may reflect a difference between mice and rats in this regard, but the two experiments make different comparisons. Whereas Collins varied sex of observers, the current experiment used male and female demonstrators for male observers.

Experiment 2

Byrne and Tomasello (1995) recently argued that, as a procedure for understanding the processes of imitative learning, the bidirectional control was limited because joystick pushes were insufficiently salient, "rather trivial sorts of behaviour". This suggests that observers may show a stronger tendency to reproduce demonstrators' behaviour if the latter were made more important or salient. Pursuing this suggestion, experiment 2 examined the possibility that the way in which the demonstrator executes the to-be-imitated response influences the probability and magnitude of matching behaviour. In previous studies, demonstrators were required merely to displace the joystick to a certain degree to obtain food reward. The magazine would operate, delivering a food pellet, as soon as criterion displacement was achieved, and under these conditions, demonstrators tend to release the joystick immediately. In experiment 2, however, half of the demonstrators were required to hold the joystick at or above the criterion angle for 0.45 s before the magazine would operate. It was anticipated that observers of these more salient responses (groups Hold-Left and Hold-Right) would show a more marked tendency than observers of rats that did not hold the manipulandum (groups No Hold-Left and No Hold-Right) to push the joystick in the same direction as their demonstrators.

Method

The method used in experiment 2 was the same as that of experiment 1a except in the following respects:

1. Subjects. Thirty-two observers were approximately 4 months old, and 16 demonstrators were approximately 8 months old, at the time of testing. All of the animals were male. They were housed in groups of four: one demonstrator, two observers of that demonstrator, and a dummy observer.

2. Apparatus. For all demonstrators, a 1000-Hz, 90-dB tone of 0.2 s duration sounded as soon as the free end of the joystick was displaced in the correct direction 7.5 cm

from its vertical starting position. For demonstrators to No Hold groups, magazine operation was initiated simultaneously with the tone, while for demonstrators to Hold groups, magazine operation was initiated 0.45 s after tone onset, provided that the degree of joystick displacement had not fallen below the 7.5-cm criterion level. Observers were not subject to a hold requirement, and for them displacement of the joystick 4 cm in either direction was immediately followed by simultaneous magazine operation and tone delivery.

3. Procedure: demonstrator training. When the demonstrators were reliably displacing the joystick 7.5 cm for food reward, those that had been assigned to Hold groups were given eight additional training sessions. The hold requirement was increased from 0 to 0.45 s in the course of the first three sessions, and maintained at 0.45 s for the remainder.

Results and discussion

While being observed, the demonstrators showed almost perfect discrimination. On average, each Hold demonstrator made 13.19 (SEM = 1.38) responses that did not meet the hold requirement and were, therefore, not reinforced.

One observer, in group No Hold-Left, failed to complete 50 reinforced responses on test and was therefore excluded from the analysis. Thus, the groups sizes were: Hold-Left = 8, Hold-Right = 8, No Hold-Left = 7, No Hold-Right = 8.

Figure 2 gives the mean discrimination ratio for each group of observers. Regardless of whether their demonstrators were subject to a hold requirement, observers of left pushing tended to push the joystick to the left more than observers of right pushing. A two-factor ANOVA (direction × hold) revealed a main effect of direction ($F_{1,27} = 9.15$, $P < 0.0054$), but no main effect of hold ($F_{1,27} = 1.52$, $P = 0.228$) or interaction ($F_{1,27} = 0$, $P = 0.995$). Pre-planned linear contrasts indicated that group Hold-Left had a stronger left bias than group Hold-Right ($F_{1,27} =$
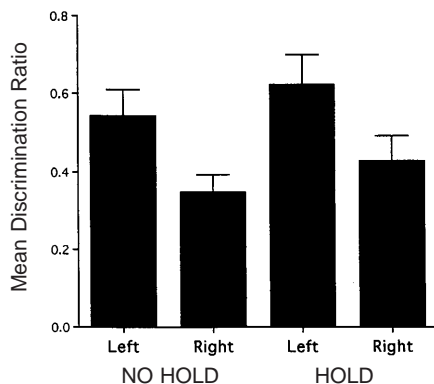
Fig. 2 Mean discrimination ratios (left responses divided by 50, the total number of test responses) for each group of observers in experiment 2. *Bars* indicate SEs

4.76, $P = 0.04$), and that group No Hold-Left had a stronger left bias than group No Hold-Right ($F_{1,27} = 4.40$, $P = 0.05$).

These results indicate that the effect of observation experience on directionality of responding in this procedure is not magnified when demonstrators hold the joystick for 0.45 s in its displaced position. The imposition of a hold requirement was expected to result in enhancement of the demonstrator-consistent responding effect by increasing the salience and distinctiveness of the demonstrators' action. No enhancement was detected, and this may have been because the hold requirement failed to increase the distinctiveness of responses for the observers, or because, while succeeding in this respect, the hold requirement also introduced a delay between responding and reinforcement. The latter explanation is implausible because in the present experiment the delay between responding and reinforcement was 0.45 s, and demonstrator-consistent responding has been observed in a previous experiment with a programmed delay of 5 s (Heyes et al. 1994).

Since the hold demonstrators regularly failed to fulfill the hold requirement, and therefore made an average of 13 non-reinforced responses in addition to 50 reinforced responses, the behaviour of Hold observers in this experiment constitutes a novel finding: observer rats showed demonstrator-consistent responding in the bidirectional control procedure even when they observed under conditions of partial reinforcement.

Experiment 3

Experiment 3 investigated the possibility that the accuracy with which demonstrators differentially respond in the reinforced direction affects the magnitude of a demonstrator-consistent responding effect. The importance of observed discriminative accuracy was suggested by experiments involving social learning of a visual discrimination problem in pigeons (Vanayan et al. 1985; Biederman and Vanayan 1988; see also Templeton 1998). Pecking a key (CS+) when an inverted triangle was illuminated resulted in access to a grain hopper. Pecks to an erect triangle (CS–) introduced a 20-s delay before a 40-s intertrial interval began. The authors found that simultaneous and successive discrimination tasks were solved more accurately by observers of partially trained, non-proficient demonstrators than observers exposed to a perfect discriminator. If, as these data suggest, discriminative performance is facilitated by exposure to the consequences of a conspecific's responses to CS–, we might expect observers to show a greater preference for the direction of their demonstrator's reinforced joystick responses when their observational experience has included nonreinforced pushes in the opposite direction. Thus, in addition to rats given standard observational experience of perfect discriminative performance by demonstrators rewarded for pushes in one direction (groups PROF-L and -R), half the observers in experiment 3 were exposed to a non-profi-

cient demonstrator that made some of its responses in the nonreinforced direction (groups NONPROF-L and -R).

Method

The method was identical to that used in experiment 1 a, except in the following respects:

1. Subjects. The subjects were 48 male hooded Lister rats. Of these, 16 were demonstrators in a previous joystick experiment and served as proficient demonstrators. The remaining 32 observers were experimentally naïve. Half of the observers served, after their test session, as non-proficient demonstrators for the remaining observers.

2. Procedure. The experiment was run in two stages. First, groups PROF-L and PROF-R were given a demonstration session in which a proficient demonstrator was reinforced for left or right responses, respectively. In the second part of the experiment, the remaining observers were also exposed to demonstrators rewarded for 50 left (group NONPROF-L) or right joystick responses (group NONPROF-R). These responses were made by non-proficient demonstrators, a subset of groups PROF-L and -R that had made 50 reinforced responses in the previous test. The non-proficient demonstrators were assigned, where possible, to observers from groups NONPROF-L and NONPROF-R against the directional bias that each animal had established in its test session. This was intended to ensure that observers of non-proficient demonstrators would observe responses in both directions. Some non-proficient demonstrators performed twice. So that these demonstrators would continue to make nonreinforced responses, the direction of reinforcement was reversed for their second demonstration session. The test phase ended when the observer had made 50 reinforced responses, or after 40 min.

Results and discussion

One of the trained demonstrators failed to make 50 reinforced responses in a demonstration session for an observer from group PROF-L, as did four naïve demonstrators (2 for group NONPROF-L, and 2 for group NONPROF-R), and therefore their observers were not tested. Of the remaining 27 observers, a further 3 (one from each of groups PROF-L, PROF-R, and NONPROF-R) failed to make 50 reinforced responses during 40 min of testing and were therefore also excluded from the analysis. Thus, for the purposes of analysis the group sizes were: group PROF-L = 6, group PROF-R = 7, group NONPROF-L = 6, group NONPROF-R = 5.

Demonstrator performance

Table 1 shows the range and number of responses demonstrators made in the nonreinforced direction. As expected,

Table 1 Range and median number of responses made in the nonreinforced direction (*L* left, *R* right) by each group of demonstrators (*PROF* proficient, *NONPROF* nonproficient) in experiment 3

Group	Median number of pushes in the nonreinforced direction	Range of number of pushes in the nonreinforced direction
PROF-L	0	0–2
PROF-R	0	0–1
NONPROF-L	7	0–26
NONPROF-R	32	5–44

many more nonreinforced responses were made by nonproficient demonstrators than proficient demonstrators, Mann-Whitney, U = 9, (n1, 2 = 13, 11), P < 0.001.

Observer performance

The mean discrimination ratios for each group of observers are shown in Fig. 3. The figure suggests that observers were influenced by the direction of reinforced joystick pushes only when few nonreinforced responses in the opposite direction were made. Analysis of variance, in which direction (left or right) and demonstrator proficiency were factors, confirmed this impression. There was a reliable main effect of direction ($F_{1,20} = 4.94$, $P = 0.038$), but not of demonstrator proficiency ($F_{1,20} = 0.025$, $P = 0.875$). While the interaction between direction and demonstrator proficiency failed to reach conventional statistical significance, ($F_{1,20} = 3.75$, $P = 0.067$), simple effects analysis of the effect of direction within each group was appropriate (Howell 1987, p. 376). Group PROF-L were found to have made a greater proportion of left responses than group PROF-R ($F_{1,20} = 9.47$, $P = 0.006$). Observers that were exposed to a mixture of responses in the reinforced and nonreinforced direction (groups NONPROF-L and NONPROF-R) produced equal numbers of left and right joystick pushes ($F_{1,20} = 0.038$, $P = 0.848$).
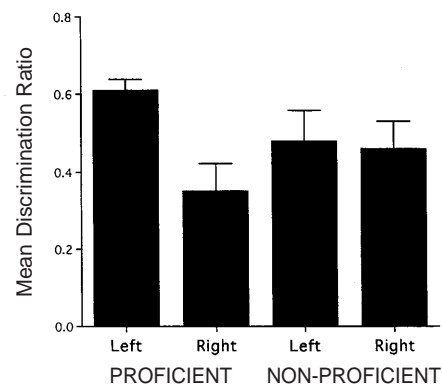
Fig. 3 Mean discrimination ratios (left responses divided by 50, the total number of test responses) for each group of observers in experiment 3. *Bars* indicate SEs

Pursuit of proficiency in instrumental performance does not seem, on the basis of these data, to be a promising variable for maximising demonstrator-consistent responding in the bidirectional control. Our rat instrumental procedure did not replicate the finding that pigeons perform a visual discrimination better if they have observed a demonstrator that makes the discrimination inaccurately when compared with observers of perfectly discriminating demonstrators (Vanayan et al. 1985; Biederman and Vanayan 1988).

However, it is of interest that, in experiment 3, matching was abolished following limited observation experience. This result has implications for the mechanisms responsible for the effects of observing non-proficient performance, and suggests that in the earlier studies with pigeons (Vanayan et al. 1985; Biederman and Vanayan 1988), the birds showed observational conditioning, i.e., learned about the relationship between a stimulus and reward. Taking in isolation Biederman's finding that discriminative performance is enhanced following observation of a non-proficient demonstrator, it is plausible that observing pecks to both positive and negative discriminative stimuli ensured that non-proficient observer pigeons were better able to tell the two stimuli apart than observers that had seen only the reinforced stimulus pecked. This would ensure that non-proficient observers performed the discrimination better because they were subsequently able to learn faster about the differential consequences of the stimuli. Alternatively, non-proficient observers could have learnt about the differential outcomes associated with CS+ and CS– during observation.

Applied to the current finding of poor discriminative performance in non-proficient observers, the first explanation is implausible because it supposes that limited preexposure to two to-be-discriminated stimuli makes those stimuli more confusable than exposure to CS+ only. With regard to the second explanation, however, it is established that, under conditions of limited exposure, information about stimulus consequences generalises between stimuli (Pavlov 1927; Hall 1991). Generalisation of information about differential outcomes between stimuli or responses would not favour behavioural matching in the bidirectional control because exposure to the positive outcome associated with, for example, left pushing would facilitate both left and right pushing, while observation of nonreinforced right pushing should suppress responses in both directions. The abolition of matching we found in observers with limited experience of non-proficient demonstrators is consistent, therefore, with the idea that observers learn about reinforcement consequences of demonstrators' actions. When applied to Biederman's findings, this suggests that his pigeons learned using an observational conditioning process.

Experiment 4

Of rat social learning paradigms to have successfully demonstrated matching behaviour of arbitrary instrumental responses, the bidirectional control is unique in having provided evidence of matching following one session of only 50 reinforced responses.

We took experiments involving rodents socially learning instrumental tasks to be most relevant to the bidirectional control procedure, and it was apparent that all had either given many more observation trials, or observation sessions, before testing for matching behaviour. 100 observation trials were given in the experiment of del Russo (1975), for example, and Denny et al. (1988) administered, on average, 232 trials to their observers. The mouse study of Collins (1988) involved three observation sessions, and experiments by Oldfield-Box (1970) tested observers following six daily sessions of social exposure. The current experiment was modelled on the Oldfield-Box (1970) procedure because it most closely resembled our own. It involved rats socially learning a leverpress response, which, like joystick pushing, is an arbitrary instrumental response.

Therefore, in an attempt to enhance matching by varying the exposure conditions of the bidirectional control, half of the observers in experiment 4 were given six daily observation sessions in addition to the one that normally occurs just before testing. Since they would have more observation training, it was anticipated that these rats (groups Multiple-Left and Multiple-Right) would show a greater tendency than rats that had observed a single session of joystick responding (groups Single-Left and Single-Right) to push the joystick in the same direction as their demonstrators.

Method

The method used in experiment 4 was the same as that of experiment 1a except in the following respects:

1. Subjects. Twenty observers were approximately 4 months old, and ten demonstrators were approximately 8 months old, at the time of testing. All of the rats were male. They were housed in groups of four: one demonstrator, two observers of that demonstrator (one in group Multiple and one in group Single), and a dummy observer.

2. Procedure: observer training and testing. The observers were trained and tested over a period of 11 days. On day 1 and each of the three subsequent days, all observers were given a session of magazine training. On day 5 and each of the 5 subsequent days, observers in the single condition were given a magazine training session, while observers in the multiple condition were given both a magazine training session and, several hours earlier, an observation session, in which their demonstrator made 50 reinforced responses to the left (group Multiple-Left) or to the right (group Multiple-Right). Magazine training was continued in this way with the intention of preventing the cues associated with food delivery from loosing secondary reinforcing properties for observers in the multiple condition. On day 11, all observers had an observation session immediately followed by a test session, as in experiment 1.
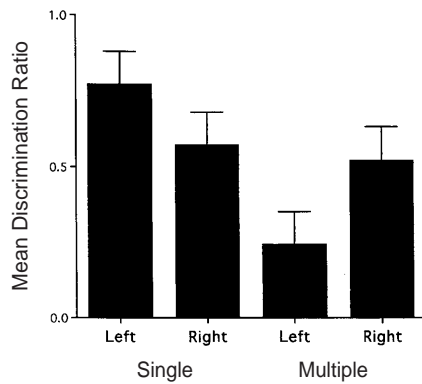
Fig. 4 Mean discrimination ratios (left responses divided by 50, the total number of test responses) for each group of observers in experiment 4. *Bars* indicate SEs

Results and discussion

While being observed, the demonstrators made no more than one response per session in the incorrect direction.

Figure 4 presents the mean discrimination ratios. It suggests that group Single-Left pushed to the left more than group Single-Right, while, in contrast, group Multiple-Left pushed to the left *less* than group Multiple-Right.

The discrimination ratios were subjected to two-factor ANOVA (direction×treatment, single vs. multiple) which confirmed that there was a main effect of treatment ($F_{1,16} = 9.8$, $P = 0.006$), but no effect of direction ($F_{1,16} = 0.18$, $P = 0.6737$). A reliable interaction between direction and treatment ($F_{1,16} = 6.4$, $P = 0.02$) was explored with simple effects analyses using the error term from the overall analysis. Group Single-Left made a greater number of left responses than group Single-Right ($F_{1,16} = 4.59$, $P < 0.05$). Group Multiple-Left pushed to the left *less* than group Multiple-Right ($F_{1,16} = 6.43$, $P < 0.05$).

The outcome of this experiment suggests that, far from enhancing the demonstrator-consistent responding effect usually observed using this procedure, increasing the number of observation training sessions results in a reversal of that effect. After an additional six, daily observation sessions, the rats tended to push the joystick in the direction opposite to that in which they had seen it being moved by their demonstrators.

The usual effect, in which observers push the joystick in the same direction, relative to the actor's body, as their demonstrators, implies that the direction of joystick movement is encoded allocentrically by the observers during observation training, i.e. with respect to the demonstrator's current location, not their own (Heyes et al. 1992; but see also Mitchell et al. 1999). In contrast, the effect reported in experiment 4, wherein rats that have been given additional observation sessions push the joystick in the opposite direction to their demonstrators, implies that by the end of their training these animals encoded the direction of joystick movement egocentrically, i.e. relative to their own location, as observers and subsequently as actors.

Extended training has long been known to have paradoxical effects on individual or "asocial" learning (Heyes et al. 1993), such as the overtraining reversal effect and the overtraining extinction effect (Mackintosh 1974), but this is, as far as we are aware, the first evidence that it can influence observational or social learning in a similar fashion.

General discussion

The results of experiments 1 and 2 extend the range of conditions in which demonstrator-consistent responding has been detected using the bidirectional control procedure. They show that such an effect occurs when (1) observer rats have had no contact with their demonstrators prior to the observation session, (2) females as well as males demonstrate for male observers (experiment 1), (3) demonstrators hold the joystick in the displaced position, rather than releasing it immediately, and (4) when demonstrators make a substantial proportion of non-reinforced responses, in addition to reinforced responses, in a single direction (experiment 2).

Experiment 3 showed that demonstrator-consistent responding in the bidirectional control is sensitive to demonstrators' discriminative accuracy, and found that observers of, for example, left pushing, themselves pushed left only when they had not seen additional unrewarded right responses. It was argued that these effects of observed non-proficiency were more readily explained in terms of learning about stimulus and response outcomes than by socially influenced attention to stimuli. It is not obvious why attention to two to-be discriminated stimuli should make their discrimination harder than attention only to the reinforced stimulus.

Experiment 4 found that observers pushed in the demonstrator-inconsistent direction following six observational training sessions. This reversal of the usual effect was interpreted as suggesting that with extensive observation experience observers code joystick movement with reference to their own position as observers, and subsequently as actors.

Mitchell et al. (1999) found that directional preference is reversed in observers tested with a joystick rotated through 180° and thereby raised the possibility that demonstrator-consistent responding by rats in this procedure is a product, not of observational learning, but of attraction to odour cues deposited by demonstrators on the joystick surface contralateral to response direction. Mitchell et al. (1999) noted that this odour hypothesis would explain some but not all of the rat bidirectional control data previously published. Similarly, some of the current data are consistent with the odour hypothesis (experiments 1–3), and others are not.

The finding, in experiments 1a and 1b, that familiar and unfamiliar females and males were equally effective demonstrators for male observers, is somewhat surprising, but not inconsistent with a scent hypothesis, suggesting an odour mechanism which is neither gender-specific, nor

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based on experience with a particular individual. Food deposits left on the joystick are plausible candidate cues according to this characterisation.

The hold requirement in experiment 2 increased the duration of contact between the demonstrator and the manipulandum and therefore may have increased odour deposits. However, the failure of this manipulation to increase demonstrator-consistent responding is, like most null results, theoretically neutral.

Non-proficient demonstrators responded both left and right in experiment 3, and this, according to an odour hypothesis, would mean they deposited odour symmetrically on the joystick, providing no odour cue for response direction. Consistent with this, our observers of non-proficient demonstrators showed no evidence of matching.

The results of experiment 4, however, cannot readily be explained in terms of attraction to residual odour on the joystick. Taking half of the counterbalanced design as an example, groups Multiple-Left and Single-Left pushed in opposite directions; group Single-Left made predominantly left responses, group Multiple-Left pushed right. The odour deposits on test should, however, have been the same for both groups. All observers had a single observation session on the test day, they were tested using the same joysticks, and the running order was counterbalanced across groups. Like observational extinction (Heyes et al. 1994), where fewer responses in a pre-trained direction are made by observers in the presence of scent cues for that direction than in their absence, reversal of demonstrator-consistent responding following extended observational training is not explicable by a simple scent hypothesis of responding in the bidirectional control.

Thus, the results of experiments 1–4 do not resolve the question of whether demonstrator-consistent responding by rats in the bidirectional control procedure represents observational learning or whether it is controlled exclusively by odour cues. However, as intended, they provide information about parameters affecting performance in this procedure that will assist further attempts to identify what role, if any, is played by imitation. In the meantime, the key question remains: whether the paucity of solid evidence of imitation in olfactory-dominant rodents, and its presence in visually dominant birds and primates, reflect evolution of imitation, or methodological problems associated with revealing imitation in olfactory dominant species. The answer to this question will, in turn, help establish whether imitation is mediated by phylogenetically general psychological processes, or whether this capacity has evolved independently in primate and avian taxa.

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