ANIMAL BEHAVIOUR, 2002, **63**, 1055–1063
doi:10.1006/anbe.2002.3007, available online at http://www.idealibrary.com on IDEAL®

Rats smell: odour-mediated local enhancement, in a vertical movement two-action test

F. M. CAMPBELL & C. M. HEYES
Department of Psychology, University College London

(Received 1 May 2001; initial acceptance 13 July 2001;
final acceptance 4 January 2002; MS. number: 6907)

In two experiments, hungry rats, *Rattus norvegicus*, were present in one side of an operant chamber while a conspecific demonstrator in the adjacent compartment moved a single lever either up or down for a food reward. During a subsequent test session, in which these rats were allowed access to the lever for the first time, all responses were rewarded regardless of their direction. In experiment 1, rats that were prevented from observing the direction of lever movement by means of a screen showed a reliable demonstrator-consistent response bias, while rats that had observed the direction of lever movement and in addition had access to any odour cues deposited on the lever did not. In experiment 2, each rat observed another rat (the 'viewed' demonstrator) moving a lever either up or down. They were then transferred into the test compartment of a different operant chamber in which another rat (the 'box' demonstrator) had moved the lever in the same direction as the viewed demonstrator or in the opposite direction. These observer rats showed a reliable preference for their box demonstrator's direction, but responded in the opposite direction to their viewed demonstrator. Taken together, the results of these experiments suggest that directional responding by rats in a vertical movement two-action test is influenced by demonstrator-deposited odour cues in addition to visual experience of a demonstrator's behaviour. Furthermore, while odour-mediated local enhancement gave rise to demonstrator-consistent responding, visual observation of a conspecific appeared to have the reverse effect.

© 2002 The Association for the Study of Animal Behaviour. Published by Elsevier Science Ltd. All rights reserved.

For over a century, psychologists and biologists have sought, with increasing rigour and sophistication, evidence that nonhuman animals are capable of some form of social learning (Galef 1988), most notably 'true imitation' (Thorndike 1898) or 'observational learning' (Hall 1963). Imitation consists of response learning by observation (Heyes 1993, 1994; Heyes & Ray 2000). It is a means by which animals acquire information about responses, actions or patterns of behaviour: how to execute them and what their consequences are. Other types of social learning consist of stimulus learning by observation (Heyes 1993, 1994). They allow animals to learn about stimuli, objects or events in the environment, their presence or location (stimulus enhancement), dynamic properties (emulation learning) and/or value (observational conditioning).

To date, the two-action test has provided the most compelling evidence of imitation by allowing animals to observe conspecific demonstrators manipulating a single object using one of two or more alternative response topographies. During a subsequent test session in which the observers are given access to the same object for the first time, responses that match those made by the demonstrator and those that do not match are rewarded. If animals engage in imitative social learning, or response learning by observation, then one would expect them to show a bias in favour of their demonstrator's response topography.

In a recent experiment using a two-action test (Whiten 1998; see also Whiten et al. 1996), four chimpanzees, *Pan troglodytes*, observed a human demonstrator opening the lid of a transparent plastic box containing food. To get the food, the demonstrator had to navigate a pair of bolts and a pair of T bars. Two of the chimpanzees observed the bolts removed before the T bars, and two the reverse sequence. Within each condition, one animal observed the bolts twisted and pulled, while the other observed the bolts being poked. On test, the chimpanzees approached the locks in the same order as their demonstrator but did not use their demonstrator's method of manipulation. These results suggest that while the chimpanzees were able to learn a stimulus sequence by observation, either they did not imitate the demonstrator's action, or the sample size was too small to reveal such an effect.

Correspondence: C. Heyes, Department of Psychology, University College London, Gower Street, London WC1E 6BT, U.K. (email: c.heyes@ucl.ac.uk).

0003–3472/02/$35.00/0 © 2002 The Association for the Study of Animal Behaviour. Published by Elsevier Science Ltd. All rights reserved.

Chimpanzees are not the only primates to have been tested for imitation using a two-action test. Voelkl & Huber (2000), for example, allowed marmosets, *Callithrix jacchus*, to observe a demonstrator using either its hands (group hand) or its mouth (group mouth) to dislodge the lids from an array of plastic canisters containing food. On test, the observers in group hand only ever opened the canisters with their hands, while the observers in group mouth used both their hands and their mouth. The behaviour of group mouth is consistent with the hypothesis that these animals were influenced by the action they observed. This interpretation is strengthened by the fact that animals with no previous observation training had a low probability of mouth opening, even when the canisters with which they were tested had previously been manipulated by a mouth demonstrator.

Studies using the two-action procedure have also provided evidence of imitation in several avian species (Japanese quail, *Coturnix japonica*: Akins & Zentall 1996; starlings, *Sturnus vulgaris*: Campbell et al. 1999; Carib grackles, *Quiscalus lugubris*: Lefebvre et al. 1997; pigeons, *Columba livia*: Zentall et al. 1996). For example, Akins & Zentall (1996) reported that naïve pigeons that had observed a conspecific demonstrator pressing a treadle with either its beak (group pecking) or its feet (group stepping) for access to food subsequently tended to manipulate the treadle using their demonstrator's response topography. The demonstrators had the same effect upon the environment (i.e. treadle depression followed by food) irrespective of whether their behaviour involved pecking or stepping. Therefore, it seems that any tendency on the part of the observers to reproduce their demonstrator's behaviour must have occurred as a result of exposure to that animal's response topography (i.e. imitative social learning) rather than to the object it manipulated (i.e. nonimitative social learning).

Thus, the results of two-action tests suggest that birds and primates can imitate motor behaviour. These are two distantly related groups of animals. If both can acquire a response through conspecific observation, then it is plausible that this ability arose via convergent evolution, or that it is a product of taxonomically general cognitive processes (Heyes 2001). In the latter case, one would expect it to be present not only in avian and primate species, but in a broad range of vertebrate taxa. To distinguish the 'convergent evolution' and 'general process' hypotheses, we need to know whether nonavian, nonprimate taxa are capable of imitation, for example rodents.

Using a variant of the two-action test called the 'bidirectional control' procedure, Heyes et al. (1992; see also Heyes & Dawson 1990) thought that they had found evidence of imitation in rats, *Rattus norvegicus*, but a subsequent study by Mitchell et al. (1999) undermined this conclusion. In this experiment, naïve rats observed demonstrators as they pushed a vertical joystick either to the left or to the right for food. The joystick was suspended directly between the two animals such that the demonstrators faced the observers and, on test, the observers confronted the joystick at an orientation different from that in which it had been viewed. For half of the observers the joystick remained in its usual position on test (group standard), while for the other half it was rotated within its mounting through an angle of 180 degrees (group rotated). The rats belonging to group standard tended to push the joystick in their demonstrator's direction, whereas the rats belonging to group rotated pushed it in the opposite direction. Taken together, these results suggest that demonstrators deposited attractive odour cues on the side of the joystick contralateral to its direction of motion and that exposure to these cues on test was sufficient to bias the direction of observer rats' responses. When the joystick was in its usual position, exploration of odour cues promoted a demonstrator-consistent response bias, but when the joystick had been rotated, exploration of odour cues promoted demonstrator-inconsistent responding.

Using an alternative two-action test, Ray & Heyes (in press) found that observer rats moved a wall-mounted lever in the same vertical direction as their demonstrator. It is possible that this effect was mediated by imitation, but Mitchell et al.'s (1999) experiment raises the possibility that it may be due instead to odour-mediated local enhancement. To distinguish these possibilities, it would be necessary independently to manipulate a rat's exposure to demonstrator-deposited odour cues and visual experience of a demonstrator's behaviour. We attempted to do this using both 'screening' (experiment 1) and 'box swapping' (experiment 2) control procedures.

EXPERIMENT 1

In experiment 1, hungry rats occupied one side of an operant chamber while a conspecific demonstrator in the adjacent compartment moved a single lever either up or down for a food reward. Of these rats, half observed their demonstrator's responses (groups up–no screen and down–no screen). The other half were prevented from doing so by means of an aluminium screen secured to the wire-mesh partition that divided the chamber into its two compartments (groups up–screen and down–screen). Once the demonstrator had finished responding, we gave each rat a test session in which it was rewarded when it moved the lever up and when it moved the lever down.

Following the results obtained by Ray & Heyes (in press), we anticipated that rats assigned to the no-screen groups would show a bias in favour of moving the lever in the same direction as their demonstrator. If this were an effect of visual cues arising from exposure to a conspecific's behaviour, rats assigned to the screen groups would not be expected to respond in the same direction as their demonstrator. If, however, the effect were due instead or in addition to demonstrator-deposited odour cues, the rats assigned to the screen groups should show a bias at least as strong as the rats assigned to the no-screen groups.

Methods

Subjects

We used 48 male hooded Lister rats obtained from Charles River (Margate, Kent, U.K.). Of these, 16 had

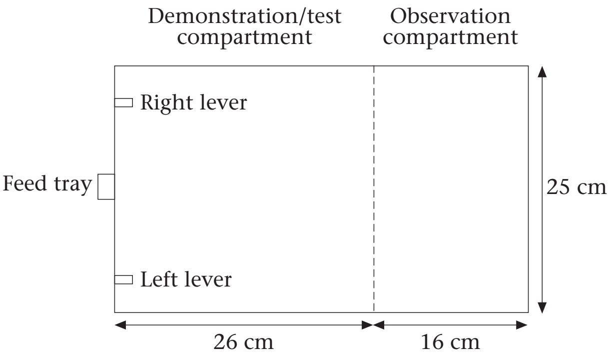

Figure 1. Plan of the vertical movement two-action test apparatus used in experiments 1 and 2. The dashed line shows the position of the wire-mesh partition.

previously served as demonstrators in a two-object/two-action test and were also used as demonstrators here. Before the experiment, these animals had an average free-feeding weight of 342 g. The remaining 32 animals were experimentally naïve and were the observers. These animals had an average free-feeding weight of 360 g.

Demonstrator and observer animals were housed separately in cages (38 × 57 cm and 27 cm high) in groups of four with water freely available. The ambient room temperature was 22°C and the light dark regime was 12:12 h (lights on at 0800 hours). Several days before the experiment, all animals were reduced to 90% of their free-feeding weight by scheduled feeding and were maintained at this level throughout the experiment by being given a restricted amount of food (Teklad TRM 9607 standard rat and mouse feed) each day. The experiment lasted ca. 2 weeks and during this period the rats showed no signs of aggression, either during or between feeding times, or distress.

Apparatus

Each rat was trained and tested in one of four identical operant chambers (42 × 25 cm and 28 cm high; Fig. 1) that were placed inside sound-attenuating boxes. The walls and ceilings of each chamber were constructed from sheet metal, and the floor was made of parallel metal rods spaced 1 cm apart. Each chamber was divided, unequally, into two compartments by a 1-cm gauge wire-mesh partition. The larger of the two compartments (26 × 25 × 28 cm) was used for demonstration and testing, while the other (16 × 25 × 28 cm) housed the observer. Both compartments could be reached by separate doors on the left of the chamber.

In the demonstration compartment, mounted on the wall directly opposite the wire-mesh partition, were two retractable levers constructed from sheet metal: one on the left and the other on the right. The levers, which were 11 cm apart, were 1.5 cm wide, 0.9 cm deep, and extended 1 cm into the chamber. They were 11 cm above floor level and 5.5 cm from the adjacent side wall. Both of the levers could be moved up towards the ceiling of the chamber and down towards the floor. At any one time, only the left or the right lever was available to the rat that occupied the demonstration compartment. The other lever was retracted and could not be reached.

We used microswitches to record lever movement, and these could be adjusted such that the extent of lever displacement necessary for a response to be registered could be varied. Demonstrators had to displace the lever by 1.5 cm for a response to be registered. Observers, in contrast, had to move the lever either up or down by 1.0 cm. Maximum displacement was required of the demonstrators to render their movements as salient as possible to the observers. We required a smaller displacement of the observers in case initial test responses were small and, when unrewarded, resulted in response extinction.

The demonstration compartment also contained a recessed food tray (4.5 × 3.5 cm) midway between the two levers and 6 cm above floor level. Whenever the subject made a response designated for reinforcement, a 45-mg sucrose pellet was delivered into the food tray. A magazine response was recorded whenever the rat's snout entered the food tray breaking a photocell beam.

The chamber was illuminated by a 24-V, 2.8-W house light in the centre of the ceiling of the demonstration compartment. The observation compartment was featureless save for an aluminium screen which could be attached to the wire-mesh partition that divided the chamber. When in place the screen completely obstructed the observer's view of the demonstration compartment.

A BBC Master computer running online Spider language controlled the equipment and collected the data.

Procedure

Each session began with the illumination of the house light and finished after 50 reinforced responses had been made or 20–30 min had elapsed (specified below), at which point the house light was extinguished.

Demonstrator training. In this experiment, each observer and demonstrator had access to only one lever. However, demonstrator training, which was conducted in preparation for a previous experiment, involved simultaneous presentation of two levers. Initially, each demonstrator received a single session of magazine training in the demonstration compartment from which the levers had been removed. During magazine training 30 food pellets were delivered on a Random Time (RT) 60-s schedule. The demonstrators were then trained, in 11 daily sessions, to manipulate either the left (N=8) or the right (N=8) lever. Within each group, half of the demonstrators were rewarded for lifting the lever up and half for pressing it down. Each of the demonstrator's training sessions lasted until the rat had made 50 reinforced responses or 20 min had elapsed.

We divided demonstrator training into two phases. During the first phase, only the left or the right lever was available to the demonstrator. Responses made to this lever in the correct direction were rewarded with food, while responses in the opposite direction had no programmed consequences. Once each demonstrator had made 90% or more of its total responses in the correct direction in each of two consecutive sessions, it entered the next phase of training. During this second phase, both levers were available to the demonstrator and only those responses on the correct lever and in the correct direction were rewarded with food. All other responses had no programmed consequences. Training continued until each demonstrator had made 90% or more of its total responses on the correct lever and in the correct direction over two consecutive sessions. This criterion was reached by all four groups after an average of 10 sessions. One rat (a right up demonstrator) was excluded from the experiment because it failed to achieve the criterion level of performance after 11 sessions. Consequently, one of the remaining right up demonstrators was assigned to four, rather than two, observer rats. The behaviour of these animals did not differ detectably from that of the other observers on test.

During the final two sessions of demonstrator training, a 'dummy' observer, of approximately the same age and weight as the demonstrator, was present in the observation compartment to ensure that demonstrator rats were accustomed to manipulating the lever in the presence of a conspecific. The demonstrators' performance was not found to be disrupted by the 'dummy' observer.

Before being observed by the rats in experiment 1, demonstrators received a single, supplementary session of training to ensure that they were accustomed to responding in the presence of one, rather than two, levers and an aluminium screen.

Observer training and testing. We assigned an equal number of rats to a demonstrator that had been trained to lift a lever up or to press it down for food. Of these rats, half observed their demonstrator's responses, while the other half did not. Thus, there were four groups of observers: up–no screen, down–no screen, up–screen and down–screen. Within each group, we counterbalanced whether the demonstrator manipulated the left or the right lever.

Before observing demonstrator performance, each observer rat received three daily sessions of pretraining. On days 1 and 3 of pretraining we gave observer rats a single session of magazine training in the test compartment during which 30 food pellets were delivered on an RT 60-s schedule. On day 2, each observer was given context training. We placed it in the observation compartment of an operant chamber for 30 min with the house light on. At no point during pretraining did observers have access to the levers.

On day 4, the test day, we placed each observer in the observation compartment of an operant chamber and left it for a 3-min acclimatization period, after which we introduced a demonstrator into the adjacent compartment. Both animals were left for a further 3 min before the houselight was illuminated, signalling the availability of reinforcement to the demonstrator. Demonstrator rats were then allowed to make 50 reinforced responses. Once a demonstrator had finished, we removed it from the operant chamber. Demonstration sessions lasted ca. 5 min. Observer rats were then transferred into the empty demonstration compartment and given a test session in which all responses were rewarded with food regardless of their direction. The interval between observation and testing was ca. 3 min, and the test session lasted 20 min.

Table 1. Responses of each group of observer rats in experiment 1

Group	*N*	$\bar{X}\pm$SE
Up–no screen	8	70.63±14.08
Up–screen	8	70.13±12.58
Down–no screen	8	64.13±16.25
Down–screen	7	81.29±13.77

Results and Discussion

Demonstrators' behaviour

During 26 of the 32 observation training sessions, demonstrator rats showed perfect discrimination. On average, five incorrect responses (range 1–13) were made in the remainder, all by group up demonstrators.

Observers' behaviour

Of the 32 observers tested, one (belonging to group down–screen) failed to make any responses on test and we excluded it from all subsequent analysis. Table 1 gives the total number of responses of each of the observers that responded on test. The rats in all four groups appeared to make an equivalent total number of responses, an impression that was supported when the data were subjected to two-way (direction × group) ANOVA. This revealed that neither the main effects nor the interaction was significant ($F_{1,27}<1$ in all cases).

We measured sensitivity to the direction of demonstrators' responses by means of a discrimination ratio. We calculated this by dividing the number of up responses by the total number of responses. A preliminary three-way (lever × direction × group) ANOVA performed on these data indicated that the main effect of, and interactions involving, the lever were not significant. Therefore, we pooled the data in Fig. 2 across rats that observed demonstrators manipulating the left lever and rats that observed demonstrators manipulating the right lever.

The observers made many more down than up responses. In addition to this bias, Fig. 2 suggests that when tested with a lever that had previously been lifted up by a demonstrator, rats made proportionately more up responses than when tested with a lever that had previously been pressed down by a demonstrator. Surprisingly, this effect appeared to be stronger when the rats' view of the demonstration compartment had been obstructed than when it was unimpeded.

Two-way (direction × group) ANOVA revealed a significant main effect of direction ($F_{1,27}=5.83$, $P=0.02$), but not of group ($F_{1,27}=2.08$, $P=0.16$). The direction × screen interaction ($F_{1,27}<1$) was not significant. Simple effects analysis using the mean squares for error from the two-way ANOVA indicated that group up–screen made

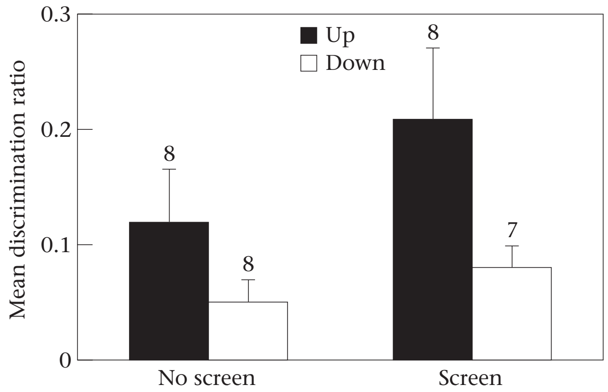

Figure 2. Mean discrimination ratio (up/up+down) for the total number of responses made by each group of observer rats in experiment 1. Vertical lines indicate standard errors. Sample sizes are given above the bars. Rats in the no-screen groups could see their demonstrators moving the level up or down; rats in the screen groups could not.

proportionately more up responses than group down–screen ($F_{1,27}$=6.00, P=0.02), whereas groups up–no screen and down–no screen did not differ ($F_{1,27}$=2.00, P=0.17).

We also calculated discrimination ratios using the first five responses made by the observer rats. This revealed that the observers' performance at the start of testing was similar to their performance across the entire test session. However, two-way ANOVA performed on these data failed to reveal any significant main effects or interactions (cf. Ray & Heyes, in press).

These results suggest that odour-mediated local enhancement occurred among rats that were prevented from observing their demonstrators' responses. In other words, it is likely that demonstrators deposited attractive odour cues on or around the surface of the lever that they manipulated, and that exposure to these cues on test was sufficient to bias the direction of naïve rats' responses. If directional responding in a two-action test were influenced solely by odour cues, then one would expect rats in both the no-screen and screen groups to show a significant bias in favour of their demonstrators' direction. In fact, rats that were permitted to observe their demonstrators' responses did not reliably respond in the same direction on test.

There are at least three alternative interpretations of the group no-screen rats' behaviour. First, demonstrators for the no-screen groups may have deposited fewer odour cues than demonstrators for the screen groups. This is unlikely if the odour cues consisted solely of saliva and food particles transferred from the demonstrator's mouth and paws to the manipulandum as an incidental consequence of lever manipulation. However, it is conceivable that cue deposition while foraging has a signalling function in rats, and in this case demonstrators for the no-screen group, which could see a conspecific while responding, may have engaged in less marking behaviour than demonstrators for the screen group, which could not see another rat while responding. Second, visual cues arising from the demonstrators' behaviour may not in themselves have given rise to learning, but may have made any deposits on the lever less attractive. Third, observation of a conspecific's behaviour may have promoted demonstrator-inconsistent responding, which counteracted the tendency towards demonstrator-consistent responding elicited by odour cues.

Demonstrator-inconsistent responding effects of this kind might be expected if, during observation training, return of the lever to rest was a more salient event than its movement in the reinforced direction. This is possible because, when the lever was being displaced, the demonstrator was standing in front of it; but when the lever was returning to rest, the demonstrator was moving towards the food tray. Alternatively, return of the lever to rest might have been learned not because it was more salient, but because it was more contiguous with the sound of magazine operation. This sound is likely to have acquired secondary reinforcing properties during observers' magazine training.

EXPERIMENT 2

In experiment 2 we used a 'box-swapping' rather than a screening procedure independently to manipulate the effects of exposure to odorous deposits and visual experience of a demonstrator's behaviour. We anticipated that this procedure would have the potential not only to replicate the effect of scent-mediated local enhancement detected in experiment 1, but also to elucidate any influence of conspecific observation.

In experiment 2, observer rats were exposed to a conspecific (the 'viewed demonstrator') that was moving a single lever in one of two directions for food. The rats were then transferred into the test compartment of a different operant chamber, in which another rat (the 'box demonstrator') had been lifting the lever up (groups up–up and down–up) or pressing it down (groups up–down and down–down) during a demonstration session that had run concurrently with that which the observers had viewed. Thus, both viewed and box demonstrators could see a conspecific while responding, and each observer rat had access to both visual information about the direction of lever movement and to odour cues on the manipulandum. For two groups of observers the visual and olfactory cues came from demonstrators moving the lever in the same direction, and for the other two groups they came from demonstrators moving the lever in different directions.

If the rats in this experiment showed a bias in favour of moving the lever in the same direction as their box demonstrator it would suggest that, even when they can see an observer while responding, demonstrators deposit sufficient odour cues on or around the lever to influence the behaviour of a conspecific that subsequently operates on that manipulandum. If the effect of viewing the demonstrator were to render demonstrator deposits less attractive, one would not expect rats to show any bias in favour of their viewed demonstrator's direction. If, in contrast, observation results in a tendency for demonstrator-inconsistent responding, then one would expect rats to respond in the opposite direction to their viewed demonstrator.

Methods

Subjects

The subjects were 80 male hooded Lister rats obtained from Charles River (Margate, Kent, U.K.). Of these rats, 16 had previously participated in a two-object/two-action test; eight as demonstrators and eight as observers. These animals were the demonstrators and at the start of the experiment had an average free-feeding weight of 345 g. The remaining 64 animals were experimentally naïve and were the observers. These animals had a free-feeding weight of 401 g. Housing and feeding conditions were the same as in experiment 1.

Apparatus

Rats were trained and tested in the same four operant chambers used in experiment 1. However, in this experiment only the left lever was made available to the rat that occupied the demonstration compartment. The right lever was retracted and remained so throughout the experiment.

Procedure

Demonstrator training. In a previous experiment, demonstrator rats had gained some experience of manipulating a lever either up and/or down for food. Before being observed by the rats in this experiment, half of the demonstrators received three sessions of training in which only up responses were rewarded. The other half received the same amount of training, but were rewarded for pressing the lever down. In experiment 2, four observer rats viewed each demonstrator.

Observer training and testing. The procedure for observer training and testing was the same as that used in experiment 1 in all respects except the following. An equal number of observer rats were assigned to one of four groups: up–up, down–up, up–down and down–down. We coded groups such that the first element referred to the direction in which the viewed demonstrator moved the lever, while the second indicated the direction of the box demonstrators' responses. For two of the groups the viewed and the box demonstrator responded in the same direction (i.e. groups up–up and down–down), while for the other two they responded in opposite directions (i.e. groups down–up and up–down).

Following group assignment, observer rats received four daily sessions of pretraining. Magazine training sessions were given on days 1 and 4 in the operant chamber where each rat would eventually observe its viewed demonstrator. Context training sessions, on the other hand, were given on days 2 and 3 in the operant chamber where each rat was to be tested.

Results and Discussion

Demonstrators' behaviour

Demonstrator rats showed perfect discrimination during 39 of the 64 observation training sessions. In the remainder, which all involved up responding, individual demonstrators never made more than one response in the nonreinforced direction.

Table 2. Responses of each group of observer rats in experiment 2

Group	*N*	$\bar{X}$±SE
Up–up	16	77.25±6.87
Up–down	16	80.31±8.14
Down–up	16	85.25±5.50
Down–down	16	77.63±5.43

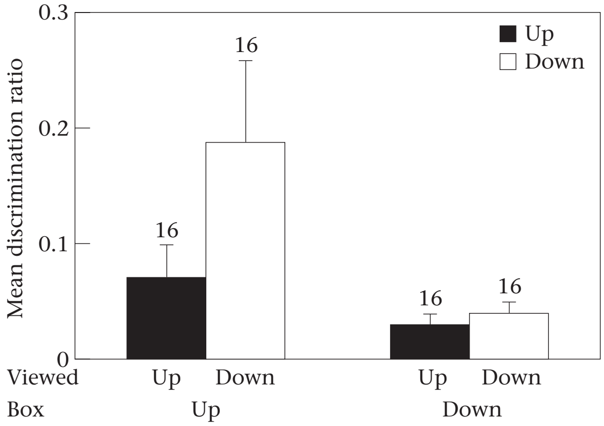

Figure 3. Mean discrimination ratio (up/up+down) for the total number of responses made by each group of observer rats in experiment 2. Vertical lines indicate standard errors. Sample sizes are given above the bars. Observers 'viewed' a demonstrator moving the lever up or down and were tested in a 'box' where the previous occupant had moved the lever up or down.

Observers' behaviour

Of the 64 rats assigned the role of observer, all responded on test. Table 2 gives the total number of their responses. The rats in all four groups appeared to make an equivalent total number of responses, an impression that was confirmed by two-way (viewed demonstrator × box demonstrator) ANOVA. This revealed that the main effect of viewed demonstrator ($F_{1,56}<1$), the main effect of box demonstrator ($F_{1,56}=1.51$, $P=0.22$) and the viewed demonstrator x box demonstrator interaction ($F_{1,56}=1.77$, $P=0.19$) were not significant.

Figure 3 shows the discrimination ratio for the total responses made by each group of observers. As in experiment 1, rats made many more down than up responses. In addition to this bias, Fig. 3 indicates an effect of the box demonstrator's direction. When tested in compartments where box demonstrators had lifted the lever up, rats made proportionately more up responses than when tested in compartments where box demonstrators had pressed the lever down. However, it appears that this bias was restricted to those rats that had observed down lever pressing. Rats that had observed up lever lifting did not tend to respond in their box demonstrator's direction. Figure 3 also suggests that there was an effect of the viewed demonstrators' direction. Rats that observed demonstrators lifting a lever up made proportionately fewer up responses than rats that observed demonstrators pressing a lever down. Again, this effect was limited in that it was detected only when the test compartment was one in which a box demonstrator had lifted the lever up. When a down-lever-pressing box demonstrator had recently vacated the test compartment, rats that observed demonstrators lifting up or pressing down did not differ.

ANOVA indicated a significant main effect of box demonstrator ($F_{1,60}$=5.41, P=0.02), whereas the main effect of viewed demonstrator ($F_{1,60}$=2.81, P=0.10) and the box demonstrator × viewed demonstrator interaction ($F_{1,60}$=1.47, P=0.23) were not significant. Simple effects analysis confirmed that group up–up made fewer up responses than group down–up ($F_{1,60}$=4.23, P=0.04), whereas groups up–down and down–down did not differ ($F_{1,60}<1$). Furthermore, group down–up made more up responses than group down–down ($F_{1,60}$=6.15, P=0.02), whereas groups up–up and up–down did not differ ($F_{1,60}<1$).

We also calculated discrimination ratios using the first five responses made by the observer rats. This revealed that the observers' performance at the start of testing was similar to their performance across the entire test session. However, two-way ANOVA performed on these data failed to reveal any significant main effects or interactions (cf. Ray & Heyes, in press).

These results suggest that a box-swapping procedure can be used to distinguish the effects of demonstrator-deposited odour cues and conspecific observation on directional responding by rats in a vertical movement two-action test. They were not, however, as straightforward as originally predicted. Following experiment 1, we anticipated that rats would respond in the same direction as their box demonstrator. This effect was confirmed, but was significant only for rats that had observed down-lever pressing. We also predicted that if visual experience of a conspecific's behaviour resulted in a tendency for demonstrator-inconsistent responding, rats would respond in the opposite direction to their viewed demonstrator. This effect was also supported, but only among rats tested in compartments where box demonstrators had lifted the lever up.

A likely explanation for this complex pattern of results is as follows. Up responding was promoted by odour cues deposited by demonstrators that lifted the lever up and by visual observation of down responding, while down responding was facilitated by odour cues left by down-responding demonstrators and by visual observation of up responding. However, because the rats in this procedure showed an extraneous bias towards pressing the lever down, a ceiling effect prevented detection of the odour and visual cues that promoted down responding. Furthermore, effects of visual and olfactory cues that facilitated up responding were detected only when they co-occurred because in cases where the visual or olfactory cue promoted down responding, the effects of the two kinds of cue cancelled one another out.

For example, groups down–up and down–down were both exposed to visual cues that resulted in a tendency to lift the lever up. They differed, however, in terms of the odour cues that they encountered on test and these deposits resulted in group down–up making proportionately more up responses than group down–down. Groups up–down and up–up, on the other hand, viewed demonstrators that resulted in down lever pressing. Consequently, any tendency towards demonstrator-consistent responding elicited by the odorous deposits to which they were exposed did not emerge.

Similarly, groups down–up and up–up both encountered odour cues that resulted in a tendency to lift the lever up, but differed in terms of their observation experience. This resulted in group up–up making proportionately fewer up responses than group down–up. Groups down–down and up–down, on the other hand, encountered odour cues on test that favoured down lever pressing and these overwhelmed any tendency towards demonstrator-inconsistent responding elicited by their observation experience.

GENERAL DISCUSSION

In experiment 1, rats that were prevented from observing the direction in which a lever was moved showed a significant demonstrator-consistent response bias when subsequently allowed access to the same lever on test. This effect, however, failed to occur among rats that had been permitted to observe their demonstrators' responses and in addition had access to any odours that were deposited on the lever. In experiment 2, rats that were tested in compartments where box demonstrators had moved the lever either up or down tended to respond in the same direction provided that their viewed demonstrators had been observed pressing the lever down. Furthermore, provided that their box demonstrators had lifted the lever up, rats whose viewed demonstrators moved a lever either up or down tended to respond in the opposite direction. Taken together, the results of experiments 1 and 2 suggest that odorous deposits are sufficient to result in a tendency for demonstrator-consistent responding by rats in a vertical movement two-action test. Visual experience of a conspecific's behaviour also had an effect, but in these experiments appeared to result in a tendency for demonstrator-inconsistent responding.

The finding that odour cues facilitated naïve rats acquiring the same pattern of behaviour as their demonstrators was not unexpected. Mitchell et al. (1999), for example, obtained evidence to suggest that in a bidirectional control procedure odours deposited by demonstrators on a vertical pole, or joystick, resulted in a tendency for demonstrator-consistent responding. Similarly, Galef & Beck (1985) reported that attraction to odour cues contributes to the tendency of rats to feed at the same sites as conspecifics. Drawing on this evidence, Ray & Heyes (in press) pointed out in their original report on the vertical two-action test that odour cues could be responsible for demonstrator-consistent and demonstrator-inconsistent behaviour in this procedure.

It is likely that in experiments 1 and 2 odour cues originated from a number of different sources including fur, saliva containing food particles and/or sweat gland secretions from a conspecific's snout and forepaws. If these deposits were attractive to other rats, they would have encouraged the observers to approach and sniff the lever on test. This, in turn, may have favoured the initiation of lever movement from an orientation that made responses in the demonstrators' direction more likely than responses in the opposite direction.

The effect of visual observation was more surprising than that of odour cues but it is not unprecedented. Ray et al. (2000), for example, found that multiple observation sessions resulted in a tendency for demonstrator-inconsistent responding by rats in a horizontal bidirectional control procedure, while Reed et al. (1996) found a similar effect for early social isolation. In the former case, it is plausible that exposure to several demonstration sessions prior to testing selectively strengthened a Pavlovian process that supported demonstrator-inconsistent responding. More specifically, the rats in these experiments may have learned by observation a stimulus–reinforcer relationship in which the stimulus was movement of the manipulandum across their visual field. In the latter case, rats reared in social isolation may have acquired the same Pavlovian relationship, not because they received extensive observation training, but because they were relatively insensitive to the odours deposited by conspecifics.

Stimulus–reinforcer learning might also have been responsible for the demonstrator-inconsistent response bias shown by rats in experiments 1 and 2. However, in this instance the stimulus was return of the lever to its resting place. Such a relationship might have been acquired either because this event was more salient than movement of the lever in the reinforced direction, or because it was more contiguous with the sound of magazine operation, a secondary reinforcer.

Our results differ from those reported by Ray & Heyes (in press). Using the same vertical bidirectional control procedure, Ray & Heyes found demonstrator-consistent, rather than demonstrator-inconsistent, responding in rats that had seen their demonstrators moving the lever, and no effect of demonstrator direction, rather than demonstrator consistency, among screen controls. Furthermore, the group effects reported by Ray & Heyes occurred at the beginning of the test session and were eradicated by the end, while we found group effects at the end of the test session and not at the beginning. However, foreshadowing the present evidence that visual cues promote demonstrator-inconsistent responding, Ray & Heyes found that rats that observed manipulation of one lever and were tested on another (which the demonstrator could not have scent marked) tended to respond up when they had seen down, and vice versa.

The only methodological difference between the two sets of studies is that our experiments used mature but slightly younger rats. However, it is unlikely that effects of odour cues and visual observation of a demonstrator vary systematically with the age of adult rats. It is more likely that the contrasting results are related to uncontrolled variation in the precise location at which demonstrators and observers deposited odour cues on the manipulandum. For example, odour cues under the manipulandum may promote up responding, while residues on the tip have little effect, and a bias in the precise location of odour cues could accumulate in the course of a day as successively tested rats are attracted to the cues deposited by their predecessors. Through this kind of cumulative effect, the results of a whole experiment could be biased by one or two demonstrators that, by virtue of their idiosyncratic response topography, deposit odour cues under the lever (leading to demonstrator consistency) or on its tip (leading to no effect of odour cues) early in the test day.

At this point we can conclude only that, while odour cues can promote demonstrator-consistent responding in a vertical bidirectional control, and visual observation can promote demonstrator inconsistency, neither effect is robust and the latter is subject to reversal. In combination with the findings of Mitchell et al.(1999), our results indicate that demonstrator-deposited odour cues affect rats' two-action test performance in complex and unpredictable ways. Consequently, it is our view that rats are not a promising species through which to examine either the mechanisms of imitation or its phylogenetic distribution. However, the vertical bidirectional control, screening and box-swapping procedures used in experiments 1 and 2 could be readily adapted for use with other species to address the question of whether imitation in birds and primates reflects taxon-general cognitive processes or convergent evolution.

Acknowledgments

This work was supported by a Biotechnology and Biological Sciences Research Council project grant to C.H., and by a University College London Graduate School Research Scholarship awarded to F.C. We are grateful to Brian Bye and Allan Stewart for animal care, to Roger Bunce for constructing the apparatus, and to Elizabeth Ray for valuable discussion throughout the project.

References

Akins, C. K. & Zentall, T. R. 1996. Imitative learning in male Japanese quail using the two-action method. *Journal of Comparative Psychology*, **110**, 316–320.

Campbell, F. M., Heyes, C. M. & Goldsmith, A. R. 1999. A demonstration of simultaneous stimulus learning and response learning by observation in the European starling using a two-object/two-action method. *Animal Behaviour*, **58**, 151–158.

Galef, B. G. 1988. Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef), pp. 3–28. Hillsdale, New Jersey: L. Erlbaum.

Galef, B. G. & Beck, M. 1985. Aversive and attractive marking of taxic and safe foods by Norway rats. *Behavioral and Neural Biology*, **43**, 298–310.

Hall, K. R. L. 1963. Observational learning in monkeys and apes. *British Journal of Psychology*, **54**, 201–226.

Heyes, C. M. 1993. Imitation, culture and cognition. *Animal Behaviour*, **46**, 999–1010.

Heyes, C. M. 1994. Social learning in animals: categories and mechanisms. *Biological Reviews*, **69**, 207–231.

Heyes, C. M. 2001. Causes and consequences of imitation. *Trends in Cognitive Sciences*, **5**, 253–261.

Heyes, C. M. & Dawson, G. R. 1990. A demonstration of observational learning in rats using a bidirectional control. *Quarterly Journal of Experimental Psychology*, **42B**, 59–71.

Heyes, C. M. & Ray, E. D. 2000. What is the significance of imitation in animals? *Advances in the Study of Behavior*, **29**, 215–245.

Heyes, C. M., Dawson, G. R. & Nokes, T. 1992. Imitation in rats: Initial responding and transfer evidence. *Quarterly Journal of Experimental Psychology*, **45B**, 229–240.

Lefebvre, L., Templeton, J., Brown, K. & Koelle, M. 1997. Carib grackles imitate conspecific and Zenaida dove tutors. *Behaviour*, **134**, 1003–1017.

Mitchell, C. J., Heyes, C. M., Dawson, G. R. & Gardner, M. R. 1999. Limitations of a bidirectional control procedure for the investigation of imitation in rats: odour cues on the manipulandum. *Quarterly Journal of Experimental Psychology*, **52B**, 193–202.

Ray, E. D. & Heyes, C. M. In press. Do rats in a two-action test encode movement egocentrically or allocentrically? *Animal Cognition*.

Ray, E. D., Gardner, M. R. & Heyes, C. M. 2000. Seeing how it's done: matching conditions for observer rats in the bidirectional control. *Animal Cognition*, **3**, 147–157.

Reed, P., Skeira, F., Adams, L. & Heyes, C. M. 1996. Effects of social isolation rearing and mirror exposure on social and asocial discrimination performance. *Learning and Motivation*, **27**, 113–129.

Thorndike, E. L. 1898. Animal intelligence. *Psychological Review Monographs*, **2**, 1–109.

Voelkl, B. & Huber, L. 2000. True imitation in marmosets. *Animal Behaviour*, **60**, 195–202.

Whiten, A. 1998. Imitation of the sequential structure of actions by chimpanzees. *Journal of Comparative Psychology*, **112**, 270–281.

Whiten, A., Custance, D. M., Gomez, J. C., Texidor, P. & Bard, K. A. 1996. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **110**, 3–14.

Zentall, T. R., Sutton, J. E. & Sherburne, L. M. 1996. True imitative learning in pigeons. *Psychological Science*, **7**, 343–346.