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Do rats in a two-action test encode movement egocentrically or allocentrically?

Received: 31 March 2001 / Revised: 17 September 2002 / Accepted: 14 October 2002 / Published online: 9 November 2002
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Abstract Two-action tests of imitation compare groups that observe topographically different responses to a common manipulandum. The general aim of the two experiments reported here was to find a demonstrator-consistent responding effect in a procedure that could be elaborated to investigate aspects of what was learned about the demonstrated lever response. Experiment 1 was a pilot study with rats of a variant of the two-action method of investigating social learning about observed responses. Groups of observer rats (*Rattus norvegicus*) saw a demonstrator push a lever up or down for a food reward. When these observers were subsequently given access to the lever and rewarded for responses in both directions, their directional preferences were compared with two 'screen control' groups that were unable to see their demonstrators' behaviour. Demonstrator-consistent responding was found to be restricted to observers that were able to see demonstrator performance, suggesting that scent cues alone were insufficient to cue a preference for the demonstrators' response direction and thereby that the rats learned by observation about body movements (imitation) or lever movement (emulation). Experiment 2 assessed responding on two levers, one that had been manipulated by the demonstrator, and a second, transposed lever positioned some distance away. Demonstrator-consistent responding was abolished when actions were observed and performed in different parts of the apparatus, suggesting that observed movement was encoded allocentrically with respect to the apparatus rather than egocentrically with respect to the actor's body. With particular reference to the influence of scent cues, the results are discussed in relation to the strengths and weaknesses of this and other varieties of the two-action procedure as tests of imitation in animals and human infants.

Keywords Egocentric encoding · Allocentric encoding · Transposition · Two-action test · Demonstrator-consistent responding

Introduction

It has taken 100 years to find a widely agreed upon answer to one question about animal imitation: how is matching behaviour that results from learning about the topography of a conspecific's behaviour (imitation) to be distinguished empirically from matching based on learning about the stimulus consequences of observed behaviour (e.g., stimulus enhancement, observational conditioning)? What had been needed was a procedure in which demonstrator-consistent responding provided evidence that animals could 'from an act witnessed learn to do an act' (Thorndike 1911). More specifically, the problem was how to control adequately for the possibility that copies of a conspecific's behaviour can be achieved by observers attending to, and learning about, the stimulus changes that actions produce.

Most commonly, imitation has been investigated using the non-exposed control method. For example, in Huang et al.'s (1983) experiment with rats, lever-pressing behaviour by observers that had seen a lever-pressing demonstrator was compared with a control group that had been confined to the apparatus prior to the test without a demonstrator present. The authors reported more frequent lever pressing in the experimental animals, and this is consistent with the idea that observers imitated the topography of lever pressing. Equally, however, enhanced lever pressing in socially exposed animals could have been the result of several psychological processes that do not involve learning about response topography. For example, observation of a demonstrators' lever responses might have increased observers' attention to the lever via a stimulus-enhancement process (Spence 1937). In this case, one might expect observers to engage in more vigorous exploratory behaviour, making chance lever-press responses more likely in these animals than in non-exposed controls. Al-

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ternatively, social exposure may have provided observers with the opportunity to learn about the affordances of the lever via emulation learning (Tomasello 1996). An understanding of the movement properties of the lever could facilitate individual learning on tests about the relationship between lever pressing and reward. According to a social facilitation hypothesis (Zajonc 1965), a conspecific's presence generates 'energizing' arousal that increases the frequency of those behaviours that a stimulus typically elicits. Pressing is a plausible unconditioned response to a lever, and therefore, Huang et al.'s observers may have been showing a social facilitation effect. A fifth possibility is that during observation, experimental observers learned an association between the lever and reward via observational conditioning (Mineka et al. 1984). If the lever becomes an appetitive conditioned stimulus for experimental observers, they would be more likely than non-exposed controls to approach the lever and make fortuitous lever-press responses that would earn a reward and be repeated.

More recently, two-action tests have been used to investigate imitation, and their increasing use in different social-learning laboratories suggests that they can provide more sound evidence of social learning about response topography (Akins and Zentall 1996; Bugnyar and Huber 1997; Campbell et al. 1998; Collins 1988; Dawson and Foss 1965; Heyes and Dawson 1990; Meltzoff and Moore 1983; Ray 1997; Voelkl and Huber 2000; Whiten 1998). Two-action tests involve two groups of observers that see a different response made to the same manipulandum. Voelkl and Huber (2000), for example, used a procedure in which a plastic canister could be pulled open in one of two ways by marmosets. Before being given access to a canister, one group of observers saw a conspecific demonstrator remove the lid to obtain food using its hands, whereas the other group saw demonstrators using their mouths to remove the lid. The authors found a demonstrator-consistent responding effect whereby observers of mouth opening used their mouths to open the canister more frequently than observers of hand opening, and hand observers only lifted the lid using their hands.

In Whiten's procedure, chimpanzees were rewarded for opening an 'artificial fruit', a transparent box containing food (Whiten 1998). Human models demonstrated how the box could be opened by removing a pair of bolts and a pair of T-bars. All four observers saw the T-bars spun or turned out of their fastenings, and one of two actions for bolt removal; the bolt was either twisted and pulled, or poked out of its lodgings. Whiten also manipulated whether bolt or T-bar removal occurred first. With regard to action sequence, chimpanzees showed a tendency to manipulate the bolts first if their demonstrator had done that first, and vice versa for T-bar removal.

Two-action tests of imitation are innovative and powerful because they compare groups that observe topographically different responses to a common manipulandum. Thus, all observers in a two-action test are exposed in the presence of another animal to the conditions necessary for socially enhanced attention to the manipulandum,

and to the relationship between the manipulandum and reward. Thus, there is equal opportunity across groups for social facilitation, stimulus enhancement, and observational conditioning about the manipulandum, and therefore these processes cannot explain the finding that each observer group preferentially uses the response they observed.

The current experiment 1 piloted a two-action test with rats that involved a vertical lever that could be pushed up or down for a food reward. The directional preferences of observers that had seen reinforced down pushing were compared with those of observers that had seen the lever pushed up for the food reward.

The general aim was to find a demonstrator-consistent responding effect in a procedure that could be elaborated to investigate aspects of what was learned about the demonstrated lever response. In particular, experiment 2 explored whether information was encoded egocentrically, as, for example, movement upward relative to the rest of the observer's body, or allocentrically, as towards some specific feature in the environment, or relative to the apparatus as a whole (Campbell 1954). In experiment 1, when a single manipulandum was used to test the effects of response observation, the egocentric and allocentric encoding hypotheses were confounded. Therefore, experiment 2 involved two bidirectional levers, one that the demonstrator contacted, and an identical lever situated in a different part of the apparatus. An effect of transposition on demonstrator-consistent responding would suggest allocentric encoding of movement (Campbell 1954). This question about the frame of reference used for encoding applies whether observers learned about body movements (imitation) or lever movements (emulation).

Experiment 1

The primary aim of experiment 1 was to establish whether a demonstrator-consistent responding effect could be found in rats with a bidirectional lever that was available during observation and testing. Group Up was exposed to a demonstrator that pushed the lever up for a food reward, and their lever responses made in a subsequent test session were compared with group Down, which had seen demonstrators making reinforced down pushes.

Experiment 1 also investigated whether scent cues deposited by demonstrators on a manipulandum could be responsible for demonstrator-consistent responding in this procedure (Mitchell et al. 1999). If, for example, the underside of a lever that has been pushed up is scent bearing, attraction to these odour deposits could explain a preference for up responses by group Up; fortuitous up responses might be more likely from beneath the lever. Thus, experiment 1 included two additional groups, group Up-Screen and group Down-Screen. During the observation session an opaque screen prevented observers in the Screen groups from seeing the responses their demonstrators were making. Failure to replicate a demonstrator-consistent responding effect in the Screen groups would sug-

gest that attraction to scent cues on the lever is an incomplete explanation for matching in the current procedure, and that observation of a demonstrator's behaviour is needed for demonstrator-consistent responding.

A screen control seemed a more appropriate method for investigating the effects of scent cues than cleaning the manipulandum in between observation and testing, as it is not possible to establish conclusively that all odour residues have been removed by cleaning. In a similar bidirectional control experiment using joysticks, Mitchell et al. (1999) examined scent effects by rotating the manipulandum for half the observers in between observation and testing. This approach was impractical given the current apparatus in which the levers could be retracted from the demonstration chamber but could not be detached and rotated.

Methods

Subjects

Forty-eight male hooded Lister rats served as subjects. The 16 demonstrators, whose free-feeding body weights ranged between 470 and 567 g, had demonstrated in a previous observational lever-press experiment. The 32 observers were experimentally naive. Their weights prior to the introduction of scheduled feeding ranged between 413 and 486 g. For the duration of the experiment, all animals were maintained at 90% of their free-feeding body weight.

Apparatus

The animals were trained and tested in four identical operant chambers. The chamber walls and ceiling were made of aluminum. Each chamber was divided into two compartments by a wire-mesh partition. The demonstration compartment measured 24×26×20 cm. The smaller observation compartment was 15×26×20 cm, and featureless. In the centre of the ceiling of the demonstration compartment was a 24-V, 2.8-W houselight. The grid floor was constructed of stainless steel rods spaced 1 cm apart. A stainless steel screen (26×20 cm) could be attached to the wire-mesh partition to obscure observers' view of the demonstration compartment.

There was a rectangular stainless steel lever in the wall of the demonstration compartment opposite the wire-mesh partition, 3 cm to the left of the centrally placed food magazine, and 11 cm above the floor. The end of the lever (1.5×1 cm) extended 1 cm from the wall. Thus, from their position in the observation compartment, observers viewed the demonstrators from behind. The lever could be displaced up or down by a maximum of 3 cm. A response was recorded if the lever moved 2 cm in either direction. A 45-mg sucrose pellet was delivered to the food magazine for each correct response (defined below). A BBC Master computer running Spider on-line control language controlled the equipment and collected the data.

Procedure

Each session began with illumination of the houselight and ended when the light went off. The houselight was extinguished immediately following the delivery of the 50th food pellet, or, if an animal failed to make 50 responses, after 1 h.

Demonstrator training. Half of the demonstrators were trained to push the lever up, and half to push it down. The demonstrators received 11 daily training sessions, and across sessions the required magnitude of deflection increased until the lever had to be moved at least 2.5 cm in the relevant direction for a response to be reinforced. Sugar was occasionally applied to the bottom of the lever to encourage up pushing. 'Dummy' observers were present in the observation compartment during the final two training sessions. These animals were not part of the experiment proper and were not tested. They were included to familiarize the demonstrators with the presence of an observer in the test chamber.

Observer training and testing. Initially observers received three daily magazine training sessions in the demonstration compartment. A random time 60-s schedule governed delivery of 30 sucrose pellets. The lever, which was not retractable, remained in the compartment during magazine training.

Immediately before its test session, each observer was placed in the observation compartment while its demonstrator made 50 up responses (groups Up and Up-Screen), or 50 down responses (groups Down and Down-Screen). For the Screen groups, an opaque screen attached to the wire-mesh partition blocked the demonstrator from view. Each correct response was followed by delivery of a food pellet to the demonstrator. Any down responses made by an up-pushing demonstrator were not reinforced, and vice versa. When a demonstrator had earned 50 sucrose pellets, it was removed from the experiment. The observer was then transferred to the demonstration compartment, and responding in either direction was reinforced until 50 reinforcers had been delivered, or 1 h had elapsed.

Results and discussion

Twelve observers failed to make 50 responses in testing, resulting in the following group sizes: group Up, $n=6$; group Down, $n=7$; group Up-Screen, $n=2$; group Down-Screen, $n=5$. Figure 1a shows observers' responses as discrimination ratios, calculated by dividing the number of up responses by 50. Despite apparent group mean differences in responding, because of large within-group variance, analysis of variance (ANOVA) failed to reveal any reliable effects: Direction ($F_{1,19}=0.317$, $P=0.58$); Screen, ($F_{1,19}=0.456$, $P=0.51$); Direction×Screen, ($F_{1,19}=3.7$, $P=0.07$).

In case group differences had declined in the course of the test session, due to non-differential reinforcement,

periment 1 but were given the opportunity to respond to two identical vertical-movement levers situated either side of, and equidistant from, the food magazine. The additional lever was introduced to investigate how information about observed lever responses was encoded.

Demonstrator-consistent responding on a lever a demonstrator had operated and on a transposed lever was compared to dissociate egocentric and allocentric hypotheses about encoding of movement information. The allocentric encoding hypothesis that information was encoded with respect to a frame of reference based on the apparatus predicts a reduced demonstrator-consistent responding effect with a transposed lever. By contrast, it is not obvious why responding should be influenced by the position of a manipulandum if topographic information was encoded egocentrically.

Methods

The method used differed from experiment 1 in the following respects.

Subjects

Forty-eight male hooded Lister rats served as observers. They had been observationally trained to push a joystick in an earlier experiment. Before the introduction of scheduled feeding, their weights ranged between 421 and 592 g. The demonstrators were those used in experiment 1.

Apparatus

The demonstration compartment contained two retractable levers with the same dimensions as the lever used in experiment 1. The position of the left lever was also the same. The right lever was attached to the wall on the right-hand side of the food magazine at the same height and distance from the magazine as the left lever.

Procedure

Observers were randomly assigned to group Up and group Down. Between two sessions of magazine training, the observers were given the opportunity to habituate to the observation compartment. With the houselight on, and the demonstration compartment empty, the observers were confined to the observation compartment for 30 min.

For half of the observers in each group, responding was demonstrated on the left lever, and the remaining half saw responses to the right lever. Only the lever to which the demonstrator was to respond was present during observation. In the subsequent test session, both levers were available to the observer. Responding in either direction and to either lever was reinforced during the test session, which ended after 50 reinforcers had been delivered.

Results and discussion

Computer error meant that no data were collected for four animals from group Up. Three animals failed to make 50 responses in testing (two from group Up, and one from group Down) and were, therefore, excluded from the analysis. Thus, the resulting group sizes were 18 and 23 for groups Up and Down, respectively. When responding throughout the test session was considered, ANOVA of observers' up discrimination ratios on the two levers failed to find any reliable effects: Direction ($F_{1,37}=0.1$, $P=0.75$); Lever ($F_{1,37}=0.08$, $P=0.78$); Direction \times Lever ($F_{1,37}=3.48$, $P=0.07$). Nor was there an effect of the counterbalancing variable, whether the demonstrator responded to the left or right lever ($F_{1,37}=1.78$, $P=0.19$).

Turning to the early part of the test session, where effects were found in experiment 1, an up/down discrimination ratio (up responses/up+down responses) was calculated separately for the lever the demonstrator had contacted and the transposed lever using observers' first five responses. In the exceptional case in which all five responses were directed to a single lever, the discrimination ratio included all responses made until both levers had been contacted at least once. This method for data inclusion was chosen to minimize missing data on the repeated measures factor (Lever). It was appropriate because the data were converted to discrimination ratios prior to analysis, and therefore, the proportion of up responses to either lever was compared within subjects, rather than the absolute number of responses.

Three animals failed to make five responses in testing (two from group Up, and one from group Down) and were, therefore, excluded from the analysis. One animal made no responses at all to the transposed lever. Six animals, three each from groups Up and Down, were excluded from analysis as statistical outliers because their discrimination ratios were more than 2 standard deviations from the group mean (Tukey 1977). Thus, the resulting group sizes were 15 and 19 for groups Up and Down, respectively.

Preliminary analysis found no effect of the counterbalancing variable, whether demonstration occurred on the left or right lever, (all $F_s < 1$, except Side \times Lever: $F_{1,30}=1.87$, $P=0.18$), and therefore, subsequent analyses disregarded this variable.

Figure 2 shows the group mean up discrimination ratios for the demonstrator-operated and transposed levers. It suggests a preference for up responses in group Up when compared with group Down, and that this preference was more marked on the lever that had been operated by the demonstrator. ANOVA revealed a main effect of direction ($F_{1,32}=6.39$, $P<0.017$), confirming that group Up made a greater proportion of up responses than group Down. Although the Direction \times Lever interaction was not reliable, ($F_{1,32}=2.72$, $P=0.1$), simple effects analysis, using an error term that comprised a weighted average of the within and between sources of error, revealed that demonstrator-consistent responding was restricted to the demonstrator-operated lever (Howell 1987). Group Up made a

performance early in the test session was also examined. Discrimination ratios were calculated across the first five test responses only. The data were partitioned in this way because a similar social-learning procedure using two unidirectional levers found effects with the first five responses (Heyes et al. 2000). Three animals from group Up-Screen failed to make five responses in testing and were excluded from the analysis.

Figure 1b shows for each group the mean proportion of the first five responses that were up pushes, and when compared with Fig. 1a suggests that the pattern of group responding was consistent across the session. ANOVA in-

dicated that, although there were no reliable main effects of demonstrator Direction ($F_{1,25}=0.43, P=0.52$) or Screen, ($F_{1,25}=3.06, P=0.092$), there was a significant interaction between direction of demonstrator responding and whether the observer's view of its demonstrator was occluded, ($F_{1,25}=6.9, P<0.015$). This interaction was examined further with simple effects ANOVA using the error term from the overall ANOVA. This showed that group Up made proportionally more up responses than group Down ($F_{1,25}=6.25, P<0.021$), and that groups Up-Screen and Down-Screen did not differ ($F_{1,25}=1.73, P=0.2$).

Thus, using a procedure that involved a vertical-movement lever that could be pushed up or down, experiment 1 found that demonstrator-consistent responding was restricted to observer groups that could see their demonstrators' actions. The absence of demonstrator-consistent responding by rats in the Screen groups suggests that, in isolation, scent cues were not sufficient to produce a preference in observers for their demonstrators' response direction.

The intention in experiment 1 was that by adopting the two-action test design, unlike a non-exposed control procedure, the opportunity for observers to learn using processes such as stimulus enhancement, social facilitation, and observational conditioning would be equal among experimental groups. All observers in groups Up and Down were exposed to the static properties of a manipulandum in the presence of a demonstrator, and because every demonstrator made lever responses of one kind or another, all these observers were exposed to dynamic properties of the manipulandum. The aim, with respect to social facilitation, was to equate observers' experience of arousal as a result of a demonstrator's presence. Similarly, it was hoped that the lever would be equally salient for groups Up and Down because they both saw it manipulated, and that this would control for the operation of stimulus-enhancement processes. In terms of the opportunity for observational conditioning to occur, all observers in groups Up and Down were exposed to 50 reinforced lever responses, and this was done with the intention of equating across groups the association between the lever and the reward. Insofar as the results of experiment 1 are not explicable in terms of scent cues (local enhancement), stimulus enhancement, social facilitation, or observational conditioning, they are consistent with the idea that observers learned by observation about response topography. However, although all observers had the opportunity to learn that the lever was movable, different movement dynamics were displayed to observers of up and down responses. It is possible, therefore, that the observers engaged in emulation learning; for example, group Up may have learned that the lever afforded upward movement.

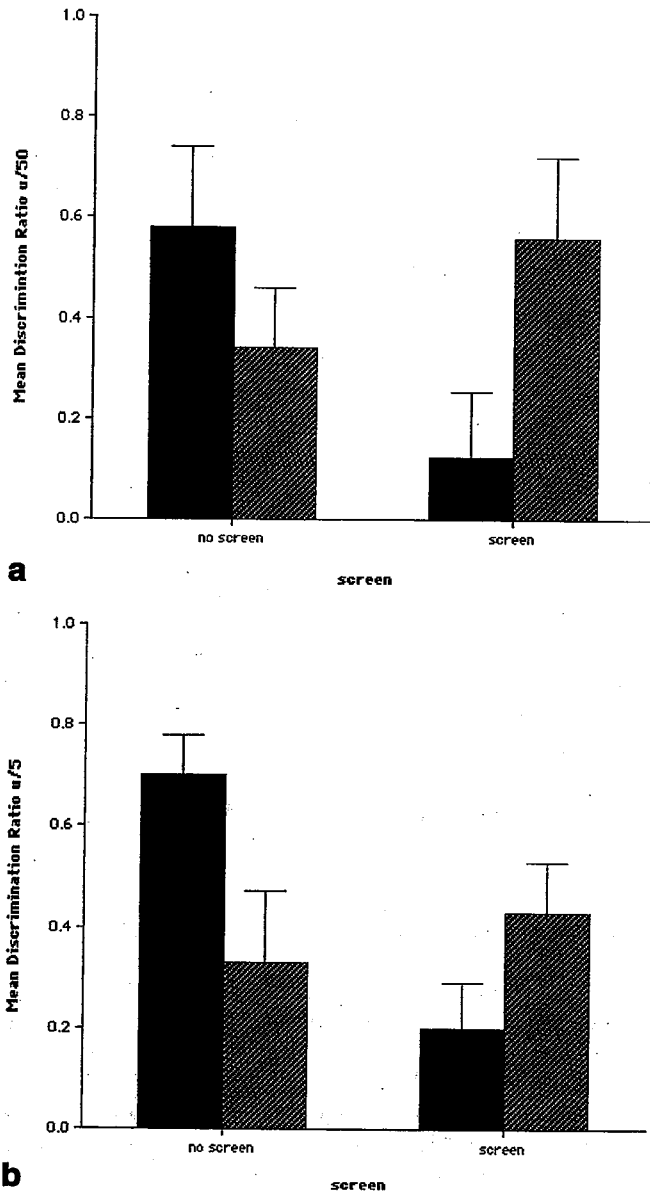


Fig. 1 a Mean discrimination ratios calculated using all responses made on test (the number of up responses divided by 50) for each group in experiment 1. b Mean discrimination ratios (the number of the first five responses that were up pushes divided by 5) for each group in experiment 1. Black bars groups Up; shaded bars groups Down

Experiment 2

In experiment 2, observers saw demonstrators respond up (group Up) or down (group Down) on one lever as in ex-

periment 1 but were given the opportunity to respond to two identical vertical-movement levers situated either side of, and equidistant from, the food magazine. The additional lever was introduced to investigate how information about observed lever responses was encoded.

Demonstrator-consistent responding on a lever a demonstrator had operated and on a transposed lever was compared to dissociate egocentric and allocentric hypotheses about encoding of movement information. The allocentric encoding hypothesis that information was encoded with respect to a frame of reference based on the apparatus predicts a reduced demonstrator-consistent responding effect with a transposed lever. By contrast, it is not obvious why responding should be influenced by the position of a manipulandum if topographic information was encoded egocentrically.

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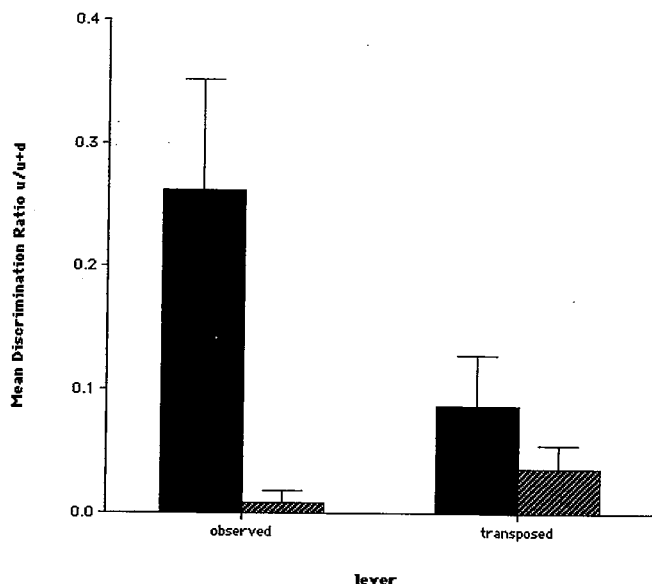


Fig. 2 Mean discrimination ratios (using either the first five responses, or all responses until both levers had been contacted once, up responses were divided by the total of up and down responses) for each group for the demonstrator-operated and transposed levers. *Black bars* Up; *shaded bars* Down

greater proportion of up responses on the lever the demonstrator had operated than did group Down ($F_{1,64}=9.185$, $P<0.001$), whereas the mean difference between groups in the proportion of up responses made on the transposed lever was not reliable ($F_{1,64}=0.37$, $P=0.55$).

It is unlikely that this effect of transposition was the result of observer neophobia with respect to the transposed lever, because the comparison between levers was of the proportion of responses in a particular direction, rather than the absolute level of responding to each lever. The effects of stimulus enhancement also do not straightforwardly predict a reduction in the *proportion* of matching responses under transposition conditions. The levers were identical in all but position, and as such, there were no non-spatial cues that identified them. Therefore, on the basis of stimulus enhancement, one would expect similar discrimination ratios on both levers.

Therefore, an effect of transposition on demonstrator-consistent responding suggests that information about response direction was lost through transposition. More specifically, it suggests that observers had encoded movement details allocentrically. An up response observed on the right lever, and encoded allocentrically as, for example, 'movement upwards, away from the food magazine, which is bottom left' would be expected to produce a weaker up preference on the transposed lever, which is to the left of the magazine. Whereas, if observers encoded movement information egocentrically, one would have expected the levers, irrespective of their position, to produce comparable demonstrator-consistent responding.

General discussion

In experiments 1 and 2, observer responding on a vertical-movement lever that had previously been operated by a demonstrator revealed a directional matching effect: observers of up pushing made a greater proportion of up responses than observers of down pushing.

Experiment 2 compared observers' directional preference on a lever previously operated by a demonstrator with responses to a second lever situated in a different part of the apparatus. Observers showed no signs of having learned about their demonstrator's behaviour under transposition conditions, suggesting that movement information was encoded allocentrically.

In general, up discrimination ratios were much lower in experiment 2 than experiment 1, with a more profound reduction in up responding by group Up. Although we have no ready explanation for this, the introduction of a second lever during testing in experiment 2 may have attenuated up responding to the demonstrator-operated lever via generalization. All test responses were reinforced, and in both groups the vast majority of responses to the transposed lever were down. If reinforcement of down responding were to generalize to the demonstrator-operated lever, one might expect a facilitation of down responses that was more apparent in group Up; floor effects in group Down may have masked some of the effects of generalization.

Response learning by observation in two-action tests

The current procedure belongs to a subset of two-action tests, bidirectional controls, in which two demonstrated actions have different effects on a manipulandum. For example, the dynamic effects on the manipulandum are different for up and down lever responses, pushes and pulls on a pendulum door (Bugnyar and Huber 1997), twists and pushes on a bolt (Whiten 1998), and left and right joystick responses (Heyes and Dawson 1990). Emulation – a term introduced by Tomasello to describe social learning about the affordances of manipulanda (Tomasello 1996) – is a plausible alternative to imitation as an explanation for demonstrator-consistent responding in bidirectional controls. We take an emulation account to suggest that, rather than learning about response topography, observers that preferentially use their demonstrator's response type in bidirectional controls may do so because they have learned by observation about the different dynamic properties of the manipulandum. In our experiment, for example, only group Up had the opportunity to learn through observation that the lever could be raised.

Whiten's (1998) data on topographic (rather than sequence) matching by chimpanzee observers in his artificial fruit procedure are interesting in this regard, because they provide some support for the hypothesis that emulation learning can occur in bidirectional control procedures. The artificial fruit has three embedded two-action

tests, and within each of these the comparison actions differ in topography. However, only in the case where the action's dynamic effects on the manipulandum differed most (a bolt that could be poked through a ring in one direction, or twisted out in another direction) was there any sign that chimpanzees showed topographic matching.

In their two-action test of imitation in quail, Akins and Zentall (1996) used a unidirectional treadle as the manipulandum. Observers saw a treadle demonstrator stepping on, or pecking at, a treadle, and when given access to the treadle themselves, tended to use the treadle action they had seen performed. By contrast with bidirectional controls, a treadle procedure is a 'different action/same motion' test, because a treadle's movement is the same whether it is pecked, or stepped upon. By controlling for simple emulation learning in this way, different-action/same-motion tests provide better evidence that observers learned about the topography of observed behaviour than bidirectional controls.

However, whereas different-action/same-motion procedures are effective in showing that observers' behaviour has been affected by the demonstrators' response topography, they may not show conclusively that this effect was mediated by response learning, rather than stimulus-learning mechanisms (Byrne 1999; Byrne and Russon 1998). In other words, an observer that reproduces an action in a different-action/same-motion procedure may do so using motor-learning processes that represent information about the topography of the observed behaviour in effector-specific form, or via perceptual-learning processes that encode what the action looked like to the observer (Cohen et al. 1990; Heyes and Foster 2002). For example, quail observers of treadle-stepping behaviour repeatedly see a 'foot-on-treadle' configuration that is perceptually transparent, that is, similar sensory input is received when treadle stepping is observed and performed (Heyes and Ray 2000). During observation, the foot-on-treadle configuration would be vicariously reinforced and, therefore, would be expected to acquire reinforcing properties of its own (Rescorla 1980). Consequently, a chance step response by a stepping observer would be rewarded, leading to observers of stepping making more step responses than observers of pecking.

A similar explanation of the tendency for pecking observers to treadle peck is implausible because the sensory input attending observation and execution of pecking is very different. However, it is not clear whether this implies that group Pecking acquired information about topography via observational response learning. The problems with group Stepping (outlined above), which is the control group for non-imitative routes to matched pecking, mean that it is not clear how observers that experienced all and only those effects associated with pecking other than its topography would behave – observers might treadle peck under these circumstances.

Thus, the advantage of different-action/same-motion two-action tests over bidirectional controls is that they provide better evidence that demonstrator topography was causal in the development of observer behaviour. How-

ever, because every action has unique stimulus correlates, it is possible that even observers in different-action/same-motion procedures learn about topography using stimulus-learning processes.

A study by Heyes et al. (1992)¹ illustrates how, in principle, bidirectional controls can be modified to provide secure evidence of social response learning about topography [olfactory cues are likely to have contaminated the imitation effect reported by Heyes et al., but not the logic of their experimental design (Mitchell et al. 1999)]. Observers were tested on a joystick transposed, more extremely than the second lever in the current procedure, so that it moved in a plane perpendicular to that observed. The authors found that demonstrator-consistent responding persisted despite the fact that, from the joystick's new position, *all* reward-correlated stimuli, static and dynamic, were uninformative with respect to the demonstrator-consistent response direction. Excluding the possibility of scent cues, this would suggest that observers learned topographic details of the observed joystick behaviour and used a social response learning mechanism to do so.

In the case of different-action/same-motion two-action tests, response-learning mechanisms would be implicated if observers reproduced two perceptually opaque actions. In this case, differences between groups in visual information about topography during observation would be unavailable to guide observers' subsequent imitative performance. This is the strength of Meltzoff's cross-target test of imitation in human infants (Meltzoff and Moore 1983) that compared frequency of a perceptually opaque action, lip protrusion, in observers following modeling of lip protrusion and mouth opening, which is also perceptually opaque.

The scent hypothesis of demonstrator-consistent responding

The pattern of simple effects in experiment 2 whereby demonstrator-consistent responding was restricted to the demonstrator-operated lever is consistent with the hypothesis that demonstrators deposited attractive scent cues on the lever. However, experiment 1 found that matching was abolished in group Screen. If scent deposits alone were insufficient to produce demonstrator-consistent responding, it seems unlikely that their absence on the transposed

¹The purpose of Heyes's experiment was to show a matching effect under conditions in which only a response learning mechanism could operate. To be convincing empirically, the decision was made to accept as imitative only examples of matching responses that were egocentrically encoded, and this was done by locating the transposed joystick in a position where no allocentric information could influence response direction. However, there is no reason to assume that imitative responses are only encoded in this way, only that allocentrically encoded imitative responses cannot be easily discriminated from responses that result from social stimulus learning. Any allocentric encoding could only have been revealed if there had also been a joystick present in the position it occupied during observation, and this was not the experiment's concern.

lever will explain why observers failed to match their demonstrators' response direction on that lever.

However, these findings do not show conclusively that demonstrator-consistent responding in experiments 1 and 2 was due to the acquisition of visual information about movement. It is possible that scent cues must summate with visual information about the manipulandum to cue a directional preference. Furthermore, a scent hypothesis can accommodate demonstrator-inconsistent responding, because directional preference is likely to depend on exactly where scent deposits are on the manipulandum, and this will vary with each demonstrator's lever action, and the history of responding across sessions. We found mean, but not statistically significant, demonstrator-inconsistent responding in (1) Screen observers in experiment 1, and (2) transposition performance across the test session in experiment 2.

The allocentric encoding hypothesis

In summary, we found a demonstrator-consistent responding effect in rats using a bidirectional control procedure, a variety of two-action test. According to current understanding of these kinds of experimental procedure, finding demonstrator-consistent responding suggests that observers socially learned about topography, and they did so using a response-based process. We have argued that this conclusion is not secure, and we discussed the individual strengths and weaknesses of the two types of two-action test procedure, bidirectional controls, and different-motion/same-action tests, as diagnostic tests for imitation. Using two bidirectional levers, experiment 2 asked about the spatial frame of reference used to encode socially acquired information. Observers showed demonstrator-consistent responding on the demonstrator-operated lever but not under transposition conditions, suggesting that movement information controlling matching responses was encoded allocentrically. This would seem to be the case whether observers learned using emulation or imitation processes. The screen control data are consistent with this hypothesis to the extent that they suggest that scent cues *alone* are insufficient to produce demonstrator-consistent responding. However, because these scent data do not conclusively rule out a role for scent cues, it might be better for the question of what is learned when a response is acquired observationally to be pursued using subject species other than rats, which are olfactory dominant (Mitchell et al. 1999). The procedure used in the present experiments could readily be modified for use with a different subject species.

Acknowledgements This research was supported by a SERC studentship. We would like to thank Roger Bunce for building the apparatus, and two anonymous reviewers for their helpful comments. The experiments were conducted in compliance with British law.

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