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Limitations of a Bidirectional Control Procedure for the Investigation of Imitation in Rats: Odour Cues on the Manipulandum

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Magazine-trained observer rats confronted a conspecific demonstrator pushing a joystick to the right or to the left for food reward before the observers were given access to the joystick from the position previously occupied by the demonstrator and rewarded for responses in both directions. For half of the observers (group 0), the joystick was in the same position when acted upon by demonstrators and observers; for the other half (group 180) the manipulandum was rotated 180° within its mounting between observation and test. As in previous experiments using this bidirectional control procedure, rats in group 0 showed demonstrator-consistent responding—that is, they pushed the joystick in the same direction, relative to the actor's body, as had their demonstrators. However, group 180 showed a reverse effect: reliable demonstrator-inconsistent responding. These results suggest that attractive odour or taste cues deposited by demonstrators on the side of the joystick contralateral to the direction of responding are sufficient to produce demonstrator-consistent responding in the bidirectional control procedure.

Heyes and colleagues (e.g. Heyes & Dawson, 1990; Heyes, Dawson, & Nokes, 1992) have reported evidence of observational learning or imitation in rats from experiments using a bidirectional control procedure. 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. When the demonstrator had made 50 reinforced responses, it was removed from the operant chamber, and the observer was given a test session in which it had access to the joystick from the position previously occupied by the demonstrator. On test, observers rewarded for responses in either

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direction 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. Conversely, the joystick moved toward the same location within the chamber when a demonstrator pushed the joystick to the right of its body and when an observer pushed the joystick to the left of its body. 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 imitation or observational learning and that they can learn a response or a response–reinforcer relationship by observation, and it was anticipated that the bidirectional control procedure would provide a basis for analytic investigation of this kind 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 naive observers when demonstrators are familiar or unfamiliar individuals, of the same or the opposite sex (Ray et al., 1998), and when 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, Jaldow, & Dawson, 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 reduces the observer's resistance to extinction to a greater extent than exposure to a demonstrator responding in the opposite direction without reinforcement (Heyes, Jaldow, & Dawson, 1993). 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 at the parameter values used in the original experiments (e.g. Heyes & 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, either in isolation or as part of factorial experiments, and a recent power analysis of such attempts estimated that a minimum of 33 observer rats per treatment group would be necessary to detect demonstrator-consistent responding in 80% of experiments (Gardner, 1997).

Research exploring alternative parameters has suggested that demonstrator-consistent responding is more likely to occur when an explicit lemon-grass scent cue is placed directly below the joystick during observation and testing. Whatever the mechanism responsible for this effect, it indicated that odour cues can have a strong influence on rats' performance in the bidirectional control procedure and thereby led us to re-examine their potential role in promoting demonstrator-consistent responding. One possibility is that odour cues are deposited asymmetrically by the demonstrator on the joystick. The snouts and paws of demonstrators almost certainly make more contact with the surface of the joystick contralateral to the direction of movement than with the ipsilateral side. If this results in a greater build-up of olfactory cues on the contralateral side, and if the observers are attracted to these cues on test, then demonstrator-consistent responding could result.

This hypothesis was tested by arranging for any deposits left on the joystick by the demonstrator during the observation period to be on the same side of the joystick (groups 0–LEFT and 0–RIGHT) or on the opposite side of the joystick (groups 180–LEFT and 180–RIGHT) during the test period. Thus, for the 180 groups, but not for the 0 groups, the joystick was rotated 180° within its mounting between observation and test. If scent cues on the joystick normally promote demonstrator-consistent responding, rats in the 180 groups would be expected to show less demonstrator-consistent responding than those in the 0 groups, and they might even show a reverse effect—that is, reliable demonstrator-inconsistent responding.

Method

Subjects

Sixty-four males PVG rats, bred at Merck, Sharp and Dohme Neuroscience Research Centre (Harlow, Essex), served as subjects; of these, 48 were observers (assigned in equal numbers to the four experimental groups), and the remaining 16 were demonstrators. The observers were experimentally naive and weighed between 200 and 270 g at the beginning of the procedure. Throughout the experiment, the animals were housed in groups of 4 (one demonstrator and its observers). The animals were fed following the last training session of each day and were maintained at 90% of their free-feeding weights.

Apparatus

The animals were trained and tested in eight operant chambers. The chambers measured 50 × 25 × 20 cm, the walls and ceilings were made of sheet-metal, and the floors consisted of metal grids.

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 joystick (0.6 cm in diameter) was suspended from the ceiling. The free end of the joystick, which was 2 cm above the floor when the joystick was in a vertical position, could only be moved to the left or the right in a plane parallel to that of the partition. The joystick, which was equidistant from the front and back panels of the box, pivoted on a potentiometer mounted above the ceiling of the chamber. Thus a current, which increased with the degree of joystick displacement, was generated. The level of signal required was set such that the joystick had to be displaced by at least 4 cm (observers) or at least 6 cm (demonstrators) to the left or to the right for a response to be recorded.

At the beginning of each observation session, 5 mg of Culpepper's Lemon Grass Essential Oil was placed into the waste tray directly beneath the joystick on a piece of plastic-backed blotting-paper (1 × 1 cm). The blotting-paper lay 6 cm below the grid floor of the operant chamber.

The demonstrator/ test compartment also contained a food tray situated at floor level equidistant from either side of the panel opposite the partition. Tray entries were recorded by an infra-red detector. A 24-V, 2.8-W bulb was used to illuminate the inside of the food tray. The tray was illuminated each time a food pellet (45 mg, mixed composition) was delivered. The observation compartment was featureless save for a loudspeaker in the ceiling adjacent to the partition. Through this loudspeaker, a 1000-Hz, 90-dB tone of 0.2-sec duration was delivered each time a joystick response was made, regardless of whether a food pellet was delivered.

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 house light and ended when the house light was extinguished. A response was scored "left" if it resulted in displacement of the joystick to the front/door side of the operant chamber, and "right" if it resulted in displacement in the opposite direction. As the demonstrators and observers faced each other on either side of the partition and the joystick, when a demonstrator made a "right" response, the joystick moved to the left in its own visual field and to the right in the observer's visual field.

Demonstrator Training. In 10 daily sessions, half of the demonstrators were trained to push the joystick to the left, and half to push it to the right. For the first four days, the joysticks were locked such that a response in the wrong direction was not possible, and the displacement necessary for the delivery of a food pellet was gradually increased until only displacements of 6 cm or more were recorded. For the remaining 6 days, the lock was removed. At the end of training, all demonstrators showed perfect discrimination.

Observer Training and Testing. The joystick was removed from the demonstration/test compartment during Days 1–4 of observer training. On Day 1, the observers were placed into the demonstrator/test compartment for a 30-min habituation period. On Day 2, they received 30 food pellets on a Random Time 60-sec schedule in the demonstration/test compartment. Each pellet delivery was accompanied by a 0.2-sec tone and illumination of the food tray. The tray light was extinguished after 2 sec or when the observer made a tray entry, whichever occurred sooner. On Day 3 the observers were given a 30-min habituation period in the observation compartment, and on Day 4 they were trained as on Day 2. On Day 5, the joystick was restored to the demonstration/test compartment, and the observers were placed into the observation compartment while their demonstrator pushed the joystick to the left (groups 0–LEFT and 180–LEFT) or to the right (groups 0–RIGHT and 180–RIGHT) for food reward on a continuous reinforcement schedule (CRF). Any responses made before the food pellet earned from the previous response had been collected were not reinforced.

Once 50 reinforced responses had been made by the demonstrator, the house light was extinguished and the demonstrator removed from the apparatus. For half of the observers (groups 180–LEFT and 180–RIGHT) the joystick was then rotated 180° within its mounting. For the other half (groups 0–LEFT and 0–RIGHT), the pole was rotated 90° in one direction and then back to its original position. In neither case was it necessary to make manual contact with any part of the aluminium pole to which rats had access on test. The house light was then illuminated, and the observer was transferred to the demonstration/test compartment, where joystick displacements of 4 cm in either direction were continuously reinforced. Failure to collect food pellets had the same consequences as for the demonstrators. The test ended once the observer had made a total of 50 reinforced responses. In order for the animals to be magazine-trained and tested at the same time of day, it was necessary to terminate the session after 30 min.

Results

Three demonstrators failed to complete their 50 reinforced responses, and therefore their observers were not tested (one from group 0–LEFT and two from group 180–RIGHT). All of the remaining demonstrators showed perfect discrimination while being observed. Nine observers (5 from group 0–LEFT, 2 from group 0–RIGHT, and one each from groups 180–LEFT and 180–RIGHT) failed to complete 50 reinforced responses within the 30-min test period and were therefore excluded from the analysis. Two animals (one from group 0–RIGHT and one from group 180–LEFT) were excluded from the analysis because their discrimination ratios were more than two standard deviations away from the group means.

A discrimination ratio was calculated for each observer by dividing the number of left responses by the total number of responses made across the test session. Figure 1 displays the group mean discrimination ratios. It would appear that the rats in group 0–LEFT made proportionately more left responses on test than did those in group 0–RIGHT, thus replicating the demonstrator-consistent responding found in previous bidirectional control experiments. However, Figure 1 also indicates that group 180–LEFT made proportionately *fewer* left responses on test than did group 180–RIGHT. A two-way ANOVA revealed no main effects of rotation or direction ($F < 1$ in both cases), but there was a reliable interaction, $F(1, 30) = 8.69$, $p < .008$). Simple effects analyses confirmed that rats in the 0 groups tended to respond in the same direction as did their demonstrators, $F(1, 30) = 3.2$, $p < 0.05$, one-tailed, whereas those in the 180 groups showed a reliable tendency to push the joystick in the opposite direction, $F(1, 30) = 5.93$, $p < .03$.

Discussion

These data suggest that odour cues deposited by the demonstrator on the joystick during the observation phase can be a major influence on the direction of joystick responding by observers in the bidirectional control procedure. It was intended that the 180° rotation of the joystick would relocate odour cues on the manipulandum such that their influence on test performance directly opposed that of any observational learning that had occurred during the demonstration period. If the rats given this treatment—the 180 groups—had merely shown less demonstrator-consistent responding than the 0 groups, it would have suggested that the effects of observational learning were being offset by those of odour cues on the joystick. Instead, however, the observers in the 180 groups showed a tendency to push the joystick in the opposite direction to their demonstrators, and this effect was at least as great as the tendency shown by the animals in the 0 groups to respond in the same direction as their demonstrators. The directional preferences found in this experiment could therefore have been due solely to odour cues deposited by the demonstrators on the side of the joystick contralateral to the direction of responding.

The odour cues may derive from saliva, containing particles of food, and/or secretions from the scent glands transferred to the joystick on the demonstrators' snouts and forepaws. The hypothesis that these cues were responsible for demonstrator-consistent responding assumes that they are attractive to observers: that the observers approached and sniffed the deposits on test and therefore tended to initiate joystick responses from a

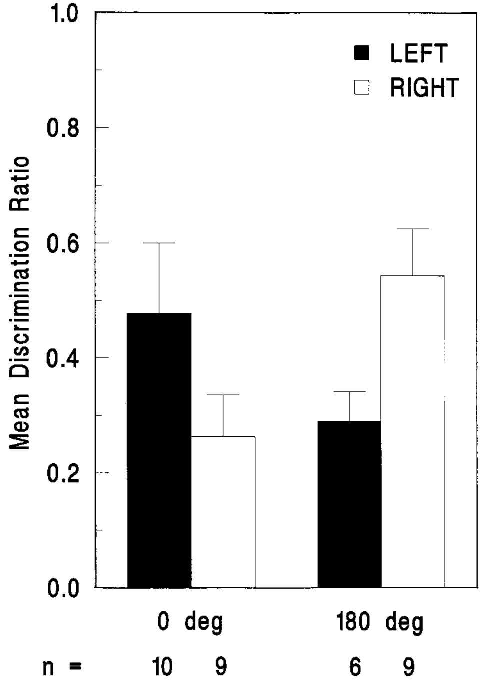

FIG. 1. Mean discrimination ratio (left/ total responses) for each observer group on test. Bar represents SEM.

location that made responses in the same direction as the demonstrator more likely than responses in the opposite direction. (It is possible that demonstrator deposits acted as taste rather than odour cues, but casual inspection of videotapes of test performance in previous bidirectional control experiments has not indicated that observer rats lick the joystick.)

The findings reported here raise the possibility that the demonstrator-consistent responding found in all previous bidirectional control experiments was due to odour deposits on the joystick, not to observational learning. The present experiment differed from previously published studies in its use of PVG strain rats and an explicit scent cue under the manipulandum, but neither of these features is likely to have been responsible for the observed effect of joystick rotation. We are not aware of any evidence that PVG rats, a pigmented strain, are especially sensitive to odour cues, and although the centrally located lemon grass stimulus may have drawn the observers' attention to the manipulandum on test and thereby magnified the effect of odour cues on the joystick, it is not clear how centrally located lemon grass could have induced demonstrator-inconsistent responding. As the lemon grass cue lay 6 cm below the floor of the chamber, it is unlikely that demonstrators could have reached it with their paws or snout and transferred the odour to the joystick. Thus, although it is conceivable that the effect of odour cues on the joystick was greater in the present experiment than in previous studies and that it masked an effect of observational learning, the present findings provide strong reason to suspect that odour cues on the manipulandum were at least partly responsible for demonstrator-consistent responding in previous experiments.

Many of the results of previous bidirectional control experiments can be explained in a straightforward way by assuming that attractive odour deposits on the joystick were responsible for demonstrator-consistent responding. For example, this hypothesis is consonant with the fact that demonstrator-consistent responding occurs when observers that have been pretrained to push in one direction are given a reversal or extinction test (Heyes & Dawson, 1990), and when joystick-naive observers are tested with a manipulandum that moves in a plane perpendicular to that in which it moved during observation (Heyes et al., 1992), or differentially reinforced on test (Ray et al., 1998), or exposed to a delay between responding and reinforcement during observation (Heyes et al., 1994).

If odour deposits on the joystick are solely responsible for demonstrator-consistent responding, it is somewhat surprising that the effect was equally strong when observers and demonstrators were housed together or apart, and when male rats observed unfamiliar male and unfamiliar female demonstrators (Ray, et al., 1998), but these findings are not in direct conflict with the odour deposits hypothesis. At most, they imply that the deposits that promote demonstrator-consistent responding are attractive to a wide range of conspecifics and are therefore more likely to consist of food particles than of gender-specific or individual-specific secretions.

The odour deposits hypothesis does not provide an obvious explanation for the findings that multiple observation sessions (Ray et al., 1998) and early social isolation of observers (Reed, Skiera, Adams, & Heyes, 1996) resulted in demonstrator-inconsistent responding, but these effects do not constitute evidence against the hypothesis. Exposure to several demonstration sessions prior to testing may selectively strengthen a Pavlovian process supporting demonstrator-inconsistent responding (e.g. learning a stimulus–reinforcer relationship in which the stimulus is movement of the joystick relative to the observer's egocentric coordinates), and rats reared in social isolation may be relatively insensitive to odours deposited by conspecifics.

Three previous findings are, however, in conflict with the hypothesis that demonstrator-consistent responding in the bidirectional control procedure is caused solely by attractive odour cues deposited on the joystick by demonstrators. First, this simple hypothesis cannot explain observational extinction (Heyes et al., 1993). In the experiment demonstrating this phenomenon, observers were pretrained to push the joystick in one direction and then exposed to a demonstrator responding in extinction in the pretrained direction (group SAME), in the non-pretrained direction (group DIFF), or confined in the apparatus with a passive conspecific (group NONE) before being tested in extinction. Taking one half of the counterbalanced design as an example, the results showed that rats pretrained to push to the left made *fewer* left responses in extinction when they had observed a demonstrator responding to the left than when they had observed a demonstrator responding to the right, and both of these groups made fewer left responses than did rats exposed to a passive conspecific prior to the test. To explain these data with reference to odour cues alone, it would be necessary to assume that demonstrators' odour deposits can, under various circumstances, both promote and inhibit responding in the demonstrators' direction.

A second anomalous experiment manipulated the observed consequences of the demonstrators' responses. Heyes, Jaldow, and Dawson (1994) found that demonstrator-consistent responding occurred when the demonstrators' responses were immediately followed by a tone and delivery of food to the demonstrator, but not when they were followed by food alone or tone alone, or when they occurred with no programmed consequences—that is, when the demonstrator was in extinction. The absence of demonstrator-consistent responding in the latter two groups can be explained by a scent deposits hypothesis if it is assumed that, when observers are attracted to the deposits, it is by the food particles that they contain. However, this adjustment to the hypothesis would not account for the absence of an effect in the food-alone condition.

Finally, in experiments in which, for technical reasons, one set of joysticks was used for demonstration sessions and a different set for observation sessions (Heyes, Jaldow, Ray, & Dawson 1994), rats that had observed a demonstrator moving a joystick (group MANUAL) showed demonstrator-consistent responding, but no systematic directional preferences were shown by rats that had observed a joystick moving automatically to the left or right (group AUTOMATIC) while alone in the chamber or with a feeding conspecific in the demonstration compartment. In these experiments, any deposits on the joysticks used for testing rats in group MANUAL would have been made by the previously tested observer, not by their demonstrator, and observers in groups MANUAL and AUTOMATIC were tested in counterbalanced order. Thus, the odour deposits hypothesis does not explain why demonstrator-consistent responding occurred in the manual condition in these two experiments.

In view of these three sets of data and of the limited nature of the current evidence favouring an odour hypothesis, we cannot conclude with confidence that demonstrator-consistent responding in the bidirectional control procedure is due solely to scent deposits on the joystick, and that imitation or observational learning does not contribute. However, the present experiment strongly implies that odour cues on the joystick are sufficient, if not necessary, to promote demonstrator-consistent responding, and therefore it indicates that it is essential to control their influence in any future studies using the procedure with rats and other olfactory-dominant species (e.g. Bugnyar & Huber, 1997; Jacoby & Dawson, 1969; Kohn, 1976). The reliance of birds on visual rather than olfactory cues means that recent attempts to demonstrate imitation learning in grackles (Lefebvre, Templeton, Brown, & Koelle, 1997), pigeons (Zentall, Sutton, & Sherburne, 1996), quail (Akins & Zentall, 1996) and starlings (Campbell, Heyes, & Goldsmith, 1998) are unlikely to have been affected by odour cues.

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Limites de la procédure de contrôle bidirectionel dans l'étude de l'imitation chez le rat: Signaux olfactifs sur le <<manipulandum>>

Des rats observateurs entraînés avec des mangeoires furent confrontés par un rat démonstrateur poussant un lévier à la droite ou à la gauche de la nourriture de récompense avant que les observateurs aient accès au levier dans la position occupé par le démonstrateur et renforcés pour une réponse dans les deux directions. Pour la moitié des observateurs (groupe 0), le levier était dans la même position quand les démonstrateurs et les observateurs lui touchait, alors que pour l'autre moitié (group 180) le levier (ou 'manipulandum' dans ce cas) fut tourné 180 degrés entre l'observation et le test. Comme dans des expériences précédentes utilisant une procédure de contrôl bidirectionel les rats du groupe 0 one montré une réponse conforme avec celle du démonstrateur, i.e. ils ont poussé le levier dans la direction, relative au corps de l'acteur, identique à laquelle les démonstrateurs l'avaient poussé. Cependant l'effet opposé fut observé dans les rats du groupe 180, i.e. une réponse opposée à celle des démonstrateurs. Ces résultats suggèrent que l'odeur et les signaux gustatifs attrayants laissés par les démonstrateurs sur le côté contralatéral à la direction de la réponse, suffisent pour produire une réponse conforme dans la procédure de contrôl bidirectionel.

Limitaciones de un procedimiento de control bidireccional para la investigación de la imitación en ratas: claves olorosas en el objeto manipulado

Se confrontó a ratas observadoras entrenadas en actividad en el comedero con una demostradora coespecífica que empujaba una vara a la derecha o a la izquierda para obtener la recompensa de comida, antes de que a las observadoras se las permitiera acceder a la vara desde la posición que previamente ocupaba la demostradora y se les recompensaran las respuestas en ambas direcciones. Para la mitad de las observadoras (grupo 0), la vara estaba en la misma posición en la que estaba para las demostradoras y las observadoras, mientras que para la otra mitad (grupo 180) el objeto manipulado se rotó 180 grados en el engaste entre la observación y la prueba. Como en experimentos previos en los que se usó este procedimiento de control bidireccional, las ratas del grupo 0 mostraron una respuesta consistente con el demostrador, es decir, empujaban la vara en la misma dirección, en relación al cuerpo del actor, como habían hecho las demostradoras. Sin embargo, el grupo 180 mostró el efecto contrario, respondiendo de manera inconsistente con la demostradora. Estos resultados sugieren que un olor atrayente o claves gustativas depositadas por las demostradoras en el lado contralateral a la dirección de la respuesta de la vara son suficientes como para producir la respuesta consistente con la demostradora en el procedimiento de control bidireccional.