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Imitation in Rats: Initial Responding and Transfer Evidence

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In two experiments, rats observed a conspecific demonstrator pushing a single manipulandum, a joystick, to the right or to the left for food reward before being given access to the joystick, for the first time, from a different orientation. In Experiment 1, rats that had observed left-pushing made more of their first three responses to the left than did rats that had observed right-pushing. In Experiment 2 the axis of joystick movement was rotated through 90° between observation and testing for half of the animals. These rats, like those that were tested with the joystick in the position it had occupied during demonstrator responding, showed a significant tendency to push the joystick in the same direction relative to their own bodies as had their demonstrators. These results, which cannot be explained in terms of stimulus–reinforcer learning, provide evidence that rats are capable of imitation, i.e. response, or response–reinforcer, learning by observation.

Almost 100 years of research on "social" or "observational" learning in animals has failed to produce a clear answer to the question of whether animals can imitate (Galef, 1988); whether they can acquire a response, or learn a response–reinforcer relationship, through observation of another animal. Evidence of this kind of observational learning has been sought

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using two basic methods. In the first and more common "non-exposed control" method, each animal in an experimental group observes the instrumental performance of a trained conspecific demonstrator, and the rate at which they subsequently acquire the same instrumental response is compared with that of a control group of animals that were not exposed to the demonstrators' behaviour. Typically, acquisition is more rapid or more complete in the experimental group, and therefore studies of this kind (e.g. Biederman & Vanayan, 1988; Kohn & Dennis, 1972; Palameta & Lefebvre, 1985) provide evidence of some sort of observational learning. However, none provides clear evidence that the facilitation effect is due to imitation, because studies that use the non-exposed method do not adequately control for the possibility that the demonstrators' behaviour has merely attracted the observers' attention to a particular part of the test environment—an effect known as "local enhancement" (Thorpe, 1963). This can facilitate subsequent response acquisition either by increasing the probability of autoshaping (Hearst & Jenkins, 1974)—i.e. learning of a stimulus–reinforcer relationship by observation—or by increasing the intensity and duration of the subjects' interaction with the manipulandum on test. In both cases, the observer animals acquire the behaviour, not by copying the demonstrators' behaviour, but through their own direct interaction with the test environment.

In common with laboratory experiments that use the non-exposed control method, the most widely cited field reports of imitation in animals (e.g. Fisher & Hinde, 1949; Kawai, 1965) do not, in fact, show that the behaviour in question was acquired through imitation rather than local enhancement (Sherry & Galef, 1984).

The second method of investigating imitation controls for local enhancement, but it has rarely been used in a systematic fashion. In this "pattern control" procedure, each observer animal is exposed to a conspecific demonstrator using one of two or more motor patterns to interact with a single manipulandum. One study of this kind provided evidence of imitation by showing that budgerigars that had observed demonstrators lifting a food cup cover with their feet were more likely to use their feet to lift the cover than birds that had observed demonstrators using their beaks (Dawson & Foss, 1965). However, subsequent studies have revealed that this effect is small, fragile, and transitory (Galef, Manzig, & Field, 1986), and, even if it were otherwise, this particular experimental procedure could not be adapted readily to permit causal analysis of the phenomenon.

Heyes and Dawson (1990) reported evidence of imitation in rats using a bidirectional control procedure—a variant of the pattern control method that will allow the kind of experimental manipulation necessary for causal analysis. During the initial phase of this procedure, each observer rat faced its conspecific demonstrator with a single manipulandum, a joystick, suspended vertically between them. In accordance with prior, conventional instrumental training, the demonstrator pushed the joystick to the right or to the left of its visual field for food reward. After this period of observation, the demonstrator was removed, and the observer was given access to the joystick from the position previously occupied by the demonstrator and rewarded for pushing the joystick in either direction. At the end of this test phase of the procedure, rats that had observed left-pushing had made more left responses than those that had observed right-pushing—that is, the observer rats showed a significant tendency to push the joystick in the same direction relative to their own bodies as had their demonstrators.

As the observer rats faced in one direction during the first phase of this experiment and in the opposite direction during the second phase, they viewed the joystick in the context of a substantially different stimulus configuration during observation and on test. This makes it likely that imitation—response learning by observation—was responsible for the observed bias in directionality of responding. However, it is possible that the rats' test performance was influenced, instead or in addition, by stimulus–reinforcer associations learned during observation. For example, as the side walls of the apparatus were constructed from different materials, the joystick might have been viewed, both during observation and on test, in conjunction with different visual cues when moved to the left and to the right. Such reward-correlated stimuli, contingent upon responding, could have played a role in strengthening those of the observers' responses that happened to match the demonstrators'. The experiments reported here tested the hypothesis that such stimulus-reinforcer learning, rather than response learning or imitation, is responsible for the bias in directionality of responding observed in the bidirectional control procedure.

EXPERIMENT 1

Rats in the bidirectional control procedure may develop in the course of a test session a tendency to make responses that match those of their demonstrators, not as a result of response or response–reinforcer learning by observation, but through response-contingent exposure to reward-correlated stimuli—that is, when, for example, an observer of left-responding makes a left response, it may be exposed to features of the apparatus that were viewed, during the observation phase, immediately prior to delivery of reward to the demonstrator, and this may account for the development of a bias in favour of left responding. However, unlike response learning, this stimulus-reinforcer account of the effect observed in the bidirectional control procedure could not fully explain the occurrence of a bias in the observers' initial responding. Consequently, in

Experiment 1 we sought evidence of response learning by observation by examining the direction of the observers' initial test responses.

Method

Subjects. Thirty experimentally naive, male, hooded Lister rats, obtained from Harlan Olac Ltd (Bicester, Oxon.) were approximately 4 months old when they served as subjects. Of these rats, 10 were randomly assigned to the role of demonstrators, and the remaining 20 were observers. Throughout the experiment observer and demonstrator animals were housed separately, in groups, with water freely available. They were fed for 90 min following each daily session.

Apparatus. The animals were trained and tested in four identical operant chambers, measuring 50 × 25 × 20 cm. The ceiling, front panel, and side panels of each chamber were made of sheet metal, and the back panel was made of clear Perspex. The floor was of a metal grid construction.

Each chamber was divided into two compartments of equal size by a 1-cm-gauge wire-mesh partition. In the compartment used for demonstrations and testing, an aluminium joystick (0.6 cm in diameter) was suspended from the middle of the ceiling. The free end of the joystick, which was 6.5 cm above the floor when the joystick was in a vertical position, could only be moved to the left or to the right in a plane parallel to that of the partition. The joystick was separated from the partition by a distance of 4 cm. This distance was chosen because it was great enough to prevent an observer rat from reaching through the partition and contacting the joystick during observation, and small enough to prevent an animal in the demonstration/test compartment from manipulating the joystick from the partition side. The latter ensured that when observers were responding on test, they were facing in the opposite direction to that from which they had viewed the demonstrators' behaviour. Microswitches were used to record movements of the joystick, and these could be adjusted so that the extent of joystick displacement necessary for a response to be registered could be varied. When demonstrators were being observed, they had to displace the free end of the joystick by at least 6 cm in order for a response to be recorded, and when observers were being tested, the necessary displacement was 3 cm.

The demonstration/test compartment also contained a food tray situated at floor level in the middle of the front panel, i.e. the panel opposite the partition. The food tray was illuminated on the inside by a 24-V, 2.8-W bulb and covered by a lightly hinged Perspex flap. A 45-mg food pellet of mixed composition was automatically delivered to the food tray whenever a subject made a correct response (variously defined below).

The other compartment, from which each subject observed its demonstrator's behaviour, was featureless save for a loudspeaker in the middle of the ceiling adjacent to the partition. Each time the pellet dispenser operated, this loudspeaker delivered a 1000-Hz, 90-dB tone of 0.2-sec duration, and the tray light went on. The light went out again the next time the tray flap closed.

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, after 50 food pellets had been delivered (unless otherwise stated), when that light was extinguished. A response was scored as "left" if it resulted in a displacement of the joystick towards the nearside of the operant chamber, and as "right" if it resulted in displacement of the joystick in the opposite direction. As observers and demonstrators faced one another on opposite sides of the partition and of the joystick, when a demonstrator made a "right" response the joystick moved to the left in the demonstrator's visual field and to the right in the observer's visual field.

1. Demonstrator training. In 16 daily sessions, half of the demonstrators were trained to push the joystick to the left and half to push it to the right. The extent of joystick displacement necessary for the delivery of a food pellet was increased gradually until, from Session 12 onwards, only displacements of 6 cm or more were rewarded. At the end of training, all demonstrators showed perfect discrimination.

2. Observer training and testing. Initially observers received three daily sessions of magazine training in the demonstration/test compartment from which the joystick had been removed; 30 food pellets were delivered on a Random Time 60-sec schedule in each session. Before being allowed access to the joystick for the first time, each observer was placed in the observation compartment while the demonstrator pushed the joystick to the left (Group LEFT) or to the right (Group RIGHT) for reinforcement. When the demonstrator had completed the session, it was removed from the apparatus, and the observer was immediately transferred to the demonstration/test compartment, where joystick displacements of 3 cm or more in either direction were reinforced. This test ended when the observer had made a total of 50 reinforced responses.

Results and Discussion

Three observer animals (two in Group LEFT and one in Group RIGHT) failed to respond within one hour of the beginning of the test period and were therefore excluded from the analysis.

We predicted that if by observation the animals learned a response or a response–reinforcer relationship, rather than a stimulus–reinforcer relationship, then they would show an initial response bias in favour of the direction to which their demonstrators had been observed pushing the joystick. This prediction was confirmed. Rats that had observed left-pushing made more of their first three responses to the left than did rats that had observed right-pushing. The mean number of left responses was 2.13 ($SD = 0.99$, $n = 8$) for Group LEFT, and 1.11 ($SD = 0.78$, $n = 9$) for Group RIGHT, $F(1, 15) = 5.55$, $p < 0.05$. Of the 17 subjects (5 in Group LEFT and 7 in Group RIGHT), 12 made their first response in the direction to which they had observed a demonstrator pushing the joystick (Fisher $p = 0.10$). One response is a small sample of behaviour, and the first response of any test session is likely to be affected by extraneous variables associated with recent handling and placement. In view of this, we assign little importance to this measure in interpreting the results of this experiment.

To assess the observers' behaviour, as did Heyes and Dawson (1990), over the entire test session, a discrimination ratio was calculated for each animal by dividing the number of left responses by the total number of responses made by the animal during the session. The mean discrimination ratio for Group LEFT was 0.68 ($SD = 0.23$, $n = 8$), and for Group RIGHT it was 0.44 ($SD = 0.36$, $n = 9$). The data were logarithm transformed to achieve homogeneity of variance before being subjected to pre-planned contrast analysis. This analysis indicated that in the course of the test session Group LEFT made more left responses than did Group RIGHT, $t(15) = 1.98$, $p < 0.05$, one-tail, and thereby showed that the effect observed by Heyes and Dawson (1990) had been replicated.

EXPERIMENT 2

In Experiment 1 rats that had observed a joystick being pushed to the left by a conspecific showed a greater initial tendency to push the joystick to the left than did rats that had observed the joystick being pushed to the right. As such an effect is unlikely to result solely from stimulus–reinforcer learning by observation, response learning is implicated. However, an initial bias toward demonstrator-consistent responding does not constitute conclusive evidence that it was the demonstrators' behaviour that influenced that of the observers. The results of an experiment in which observational discrimination training occurred in the absence of conspecific demonstrators (Denny, Clos, & Bell, 1988) raise the possibility that the movement of the joystick effected by the demonstrators' behaviour, rather than the behaviour itself, may have influenced the observers' test performance. In this study, prior to being given access to a joystick manipulandum, rats observed the joystick being moved automatically to both the right and left of its vertical starting position. For half of the animals the left movement signalled the delivery of food to the observer (S+) and the right movement signalled food omission (S−); the other half of the animals had the reverse assignment. Five of the six rats tested made their first response in the S+ direction, an effect that Denny et al. (1988) attributed to "purposeful" action following stimulus–reinforcer contingency learning.

Experiment 2 used a transfer test to establish whether the demonstrators' behaviour, rather than its effects on the joystick, is responsible for the bias in directionality of responding observed using the bidirectional control procedure. As in previous experiments, during the observation phase of the procedure all subjects observed the joystick being pushed by a demonstrator to the right or to the left in a plane parallel to the partition dividing the demonstration/test compartment from the observation compartment. However, for half of the subjects, before the test phase the joystick was moved to one side of the demonstration/test compartment, where it could be pushed to the right or to the left in a plane parallel to the side wall, and therefore perpendicular to the plane through which it had been moved by the demonstrators.

As Figure 1 illustrates, relocation of the joystick ensured that rats that had observed left pushing, but not those that had observed right pushing, could push the joystick towards the same corner of the box as had their demonstrators—a response that would now be labelled "right". Con-

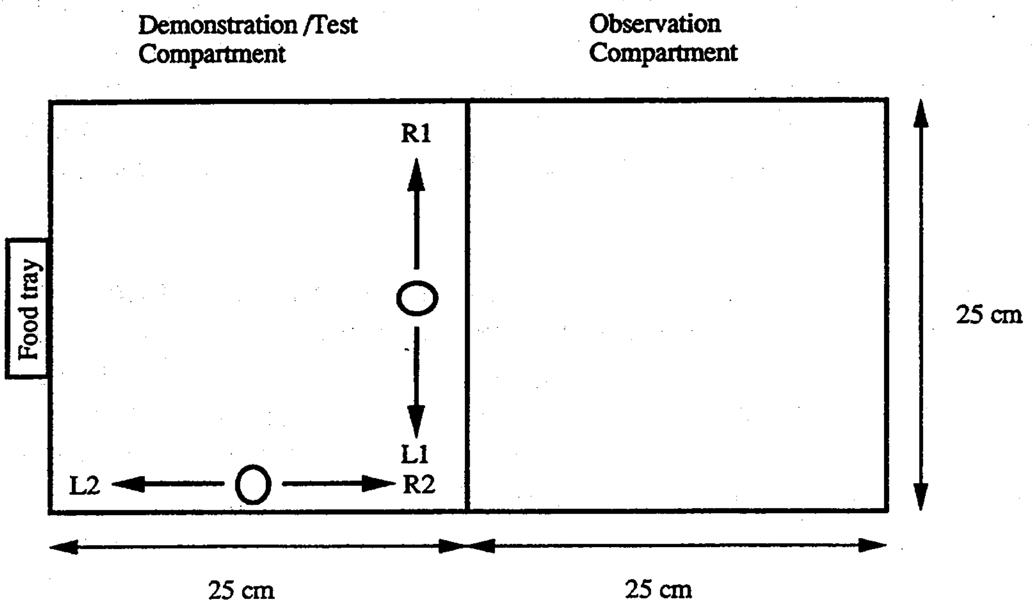

FIG. 1. Plan of the apparatus used in Experiment 2, showing the position and plane of movement of the joystick during the observation phase, and the test phase for STANDARD groups (L1, R1), and during the test for PERPENDICULAR groups (L2, R2). Responses effecting movement of the joystick toward locations marked L were scored as "left", and responses effecting movement towards locations marked R were scored as "right".

sequently, if the directionality of observers' responding is influenced by stimulus–reinforcer learning during observation, one would expect rats that have observed left pushing to push to the right more during the transfer test than rats that have observed right pushing. In contrast, if the directionality of observers' responding is influenced by response learning during observation, one would expect rats that have observed left-pushing to push to the left more during the transfer test than those that have observed right-pushing. Such an effect would indicate that observer rats tend to push the joystick in the same direction relative to their own bodies as did their demonstrators.

The latter prediction was guided by the results of a pilot study in which 8 animals that had been trained by conventional methods to push the joystick to the left or to the right of its original position were given one 50-response test session with the joystick in its new position. During this session both left and right responses were reinforced. Of the 8 animals, 4 showed perfect transfer, i.e. for each of the 50 responses the rats pushed the joystick in the same direction relative to their own bodies as they had during training. The remaining 4 animals made a maximum of three responses in the opposite direction.

Method

Subjects. Forty male, hooded Lister rats, obtained from Harlan Olac Ltd. (Bicester, Oxon.) were approximately 3 months old when they served as subjects; 8 rats were randomly assigned to the role of demonstrators, and the remaining 32 were observers. Throughout the experiment the animals were housed in groups of 5 (one demonstrator plus its 4 observers), with water freely available. They were fed for 90 min following each daily session.

Apparatus and Procedure. The apparatus and procedure were the same as those used in Experiment 1, except in the following respects. The observers were randomly assigned to one of four groups: LEFT–STANDARD, LEFT–PERPENDICULAR, RIGHT–STANDARD, and RIGHT–PERPENDICULAR. The treatment of Groups LEFT–STANDARD and RIGHT–STANDARD was identical to that of Groups LEFT and RIGHT in Experiment 1. For Groups LEFT–PERPENDICULAR and RIGHT–PERPENDICULAR the location of the joystick was changed after the observation phase and before the observers were tested. In its new location (see Figure 1) the joystick hung from the ceiling 4 cm away from the near side wall of the demonstration/test compartment, and half-way between the front panel (containing the food tray) and the partition dividing the demonstration/test compartment from the observation compartment. In this position, the joystick could be moved only in a plane parallel to the side wall and therefore perpendicular to the plane through which it had been moved by the demonstrator. During the observation phase, demonstrators' responses that resulted in the joystick moving toward the far side wall of the demonstration/test compartment were scored as "right", and those that resulted in the joystick moving toward the near side wall were scored as "left". During the test phase, responses made by rats in Groups LEFT–STANDARD and RIGHT–STANDARD were coded in the same way as those of the demonstrators, but for Groups LEFT–PERPENDICULAR and RIGHT–PERPENDICULAR responses that resulted in movement of the joystick towards the front panel were scored as "left", and those that resulted in movement of the joystick toward the partition (and therefore into the same corner of the compartment as had left responses during the observation phase) were scored as "right".

Results and Discussion

We predicted that if the rats learned a response through observation, they would show a bias in favour of pushing the joystick in the same direction relative to their own bodies as had their demonstrators, regardless of whether the joystick was in the standard or the perpendicular position on test. Given the way in which responses were scored in this experiment, such a tendency would be apparent if the LEFT groups made more left responses on test than the RIGHT groups. The results confirmed this prediction.

Four animals did not complete the test session and were therefore excluded from the analysis. Of these rats, which did not obtain 50 reinforcers within one hour of the beginning of the test, one was in Group LEFT–STANDARD, one in Group RIGHT–STANDARD, and two in Group RIGHT–PERPENDICULAR. A discrimination ratio was calculated for each of the remaining observer animals by dividing the number of left responses by the total number of responses made in the test session. These data, which are represented in Figure 2, were subjected to a two-way analysis of variance, which revealed that observers in the LEFT groups made more left responses than observers in the RIGHT groups, $F(1, 24) = 18.11$, $p = 0.0003$, but showed no effect of the STANDARD–PERPENDICULAR variable and interaction ($F < 1$ in both cases).

GENERAL DISCUSSION

Following those of Heyes and Dawson (1990), these results suggest that rats are capable of imitation, that is, of learning a response, or a response–reinforcer, relationship by observation. They show that in the context of a bidirectional control procedure rats tend to push a joystick in the same

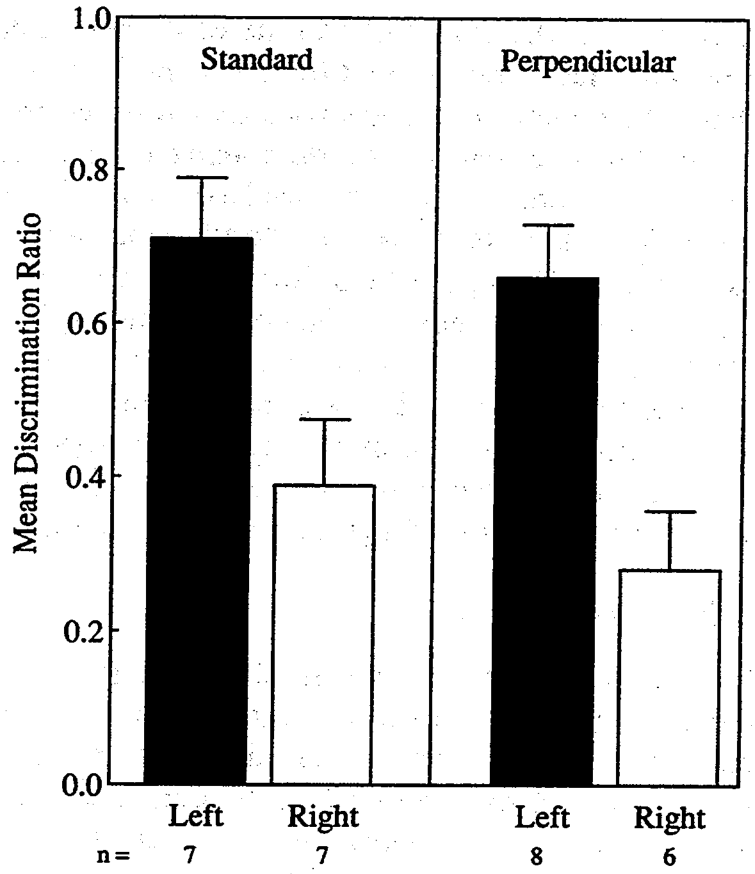

FIG. 2. Mean discrimination ratios, and their standard errors, for the four groups in Experiment 2. Ratios were calculated by dividing the number of left responses by the total number of responses.

direction relative to their own bodies as had their demonstrators (1) on initial contact with the manipulandum (Experiment 1), and (2) when the joystick moves through a plane perpendicular to that in which it was moved by the demonstrators (Experiment 2).

Denny et al. (1988) reported that after observing a joystick moving automatically, rats pushed it for the first time in the direction that had signalled reward during observation. This raises the possibility that observation of automatic joystick movement would be an appropriate control for stimulus–reinforcer learning, but we believe that the transfer procedure used in Experiment 2 provides a stronger test. If observation of automatic movement and conspecific-generated movement had equivalent effects on behaviour, it would indicate that in the latter case the effect *could* be mediated by stimulus–reinforcer learning. In contrast, successful transfer in Experiment 2 *could not* be mediated by stimulus–reinforcer learning, and therefore this account is ruled out empirically.

The significance of the present findings, and the potential utility of the bidirectional control procedure, are highlighted by recent evidence which threatens to undermine the traditional assumption (Thorndike, 1898) that birds (Sherry & Galef, 1990) and primates (Fragaszy & Visalberghi, 1989; Visalberghi & Fragaszy, 1990) are capable of non-vocal imitation.

REFERENCES

Biederman, G.B., & Vanayan, M. (1988). Observational learning in pigeons: The function of quality of observed performance in simultaneous discrimination. *Learning & Motivation, 19*, 31–43.

Dawson, B.V., & Foss, B.M. (1965). Observational learning in budgerigars. *Animal Behaviour, 13*, 470–474.

Denny, M.R., Clos, C.F., & Bell, R.C. (1988). Learning in the rat of a choice response by observation of S–S contingencies. In T.R. Zentall & B.G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 207–223). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Fisher, J., & Hinde, R.A. (1949). The opening of milk bottles by birds. *British Birds, 42*, 347–357.

Fragaszy, D.M., & Visalberghi, E. (1989). Social influences on the acquisition of tool-using behaviors in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 103*, 159–170.

Galef, B.G. (1988). Imitation in animals: History, definition and interpretation of data from the psychological laboratory. In T.R. Zentall & B.G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Galef, B.G., Manzig, L.A., & Field, R.M. (1986). Imitation learning in budgerigars: Dawson and Foss (1965) revisited. *Behavioral Processes, 13*, 191–202.

Hearst, E., & Jenkins, H.M. (1974). *Sign-tracking: The stimulus–reinforcer relation and directed action*. Austin, TX: Psychonomic Society.

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.

Kawai, M. (1965). Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Inlet. *Primates, 6*, 1–30.

Kohn, B., & Dennis, M. (1972). Observation and discrimination learning in the rat: Specific and nonspecific factors. *Journal of Comparative and Physiological Psychology, 78*, 292–296.

Palameta, B., & Lefebvre, L. (1985). The social transmission of a food-finding technique in pigeons: What is learned? *Animal Behaviour, 33*, 892–896.

Sherry, D.F., & Galef, B.G. (1984). Cultural transmission without imitation: Milk bottle opening by birds. *Animal Behaviour, 32*, 937–938.

Sherry, D.F., & Galef, B.G. (1990). Social learning without imitation: More about milk bottle opening by birds. *Animal Behaviour, 40*, 987–989.

Thorndike, E.L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Review Monographs, 2*, No. 8.

Thorpe, W.H. (1963). *Learning and instinct in animals*. London: Methuen.

Visalberghi, E., & Fragaszy, D.M. (1990). Food-washing behaviour in tufted capuchin monkeys, *Cebus apella*, and crabeating macaques, *Macaca fascicularis*. *Animal Behaviour, 40*, 829–836.

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L'imitation chez le rat: réponse initiale et évidence de transfert

Dans deux expériences, les rats observaient un congénère ("démonstrateur") poussant un manipulandum unique, une manette, vers la droite ou vers la gauche pour obtenir de la nourriture avant d'avoir pu avoir accès à la manette, pour la première fois, à partir d'une orientation différente. Dans l'expérience 1, les rats qui avaient observé que la manette était poussée à gauche produisaient plus de réponses à gauche qu'à droite, parmi les trois premières, et plus que des rats qui avaient observé la manette poussée à droite. Dans l'expérience 2, l'axe du mouvement de la manette était tourné de 90° entre l'observation et le test pour la moitié des animaux. Ces rats, de même que ceux qui étaient testés avec la manette dans la position qui était utilisée pendant la démonstration, montraient une tendance significative à pousser la manette dans la même direction par rapport à leur propre corps, de la même façon que les rats "démonstrateurs". Ces résultats qui ne peuvent pas être expliqués en termes d'apprentissage stimulus-renforcement, démontrent que les rats sont capables d'imitation, c'est-à-dire d'apprentissage de réponse, ou de réponse-renforcement, par observation.

Imitación en ratas: Respuesta inicial y evidencia de transferencia

En dos experimentos, ratas observaron como un demostrador de la misma especie empujaba un manipulandum único (un "joystick") hacia la derecha o la izquierda para obtener una recompensa (comida) antes de obtener acceso al joystick, por la primera vez, desde una orientación diferente. En el primer experimento, ratas que habían observado movimientos del joystick hacia la izquierda del demostrador hicieron una proporción mayor de sus primeras tres respuestas hacia la izquierda que aquéllas que habían observado movimientos hacia la derecha. En el segundo experimento, el eje del movimiento del joystick fue rotado 90° entre la observación y el ensayo para la mitad de los animales. Tanto estos individuos como aquéllos que encontraron el joystick en la misma posición en la que había estado cuando lo utilizaba el demostrador mostraron una tendencia significativa a empujar el joystick en la misma dirección con respecto a sus propios cuerpos que aquélla en la que lo habían empujado sus demostradores. Estos resultados, que no pueden ser explicados en términos de aprendizaje de estímulo-reforzador, proveen evidencia de que las ratas son capaces de imitación, esto es de aprendizaje por observación de respuestas, o de apareamientos respuesta-reforzador.