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Imitation in rats (*Rattus norvegicus*): The role of demonstrator action

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Abstract

In a bidirectional control procedure, rats had their first opportunity to push a joystick immediately after observing, from an adjacent compartment, the joystick moving 50 times either to the right or to the left, with each movement signalling the delivery of inaccessible food. Half of these animals observed the joystick moving automatically, and half observed a conspecific demonstrator pushing the joystick. When they were given direct access to the joystick, the observers were rewarded for both left and right pushes. Rats that had observed the joystick moving through the action of a conspecific demonstrator showed a response bias in favour of the observed direction of joystick movement (Experiment 1), while rats that had observed the joystick moving automatically, either in the presence or absence of a passive conspecific, did not show observation-consistent responding (Experiments 1 and 2). These results apparently confirm that rats are capable of imitation or observational learning.

Key words: Observational learning; Social learning; Imitation; Rat

Introduction

Imitation differs from other forms of social learning in terms of what is learned as a direct result of observation or interaction with another animal (typically a conspecific) or its products (e.g. scent marks, discarded food items) (Heyes, 1993, 1994). In non-imitative social learning, observers learn about stimuli, objects or events in the environment, either to distinguish them from other classes of stimuli or that they have a positive or negative

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value by virtue of their relationships with other objects and events. For example, rhesus monkeys, *Macaca mulatta*, avoid snakes (i.e. snakes acquire a negative value for them) after they have observed a conspecific behaving fearfully towards snakes (Cook et al., 1985), and distinctive diets become attractive to rats when their odour has been detected on the breath of a conspecific (Galef and Stein, 1985). In imitative social learning, on the other hand, observers learn as a direct result of conspecific observation about responses, actions, or patterns of behaviour. Observers may acquire the plan, or 'impulse' (Thorndike 1898) for a behaviour pattern, and/or learn that a certain behaviour pattern has a particular consequence or outcome (Mackintosh, 1983). The former effect is sometimes called 'copying' (Galef, 1988), and is common among passerine birds that acquire species- or locale-specific song from conspecifics (e.g. Petrinovich, 1988). The latter has been termed 'observational learning' (Hall, 1963), 'reflective imitation' (Morgan, 1900) and 'true imitation' (Thorpe, 1956).

Evidence from two sources has recently cast doubt on the view, originally expressed by Thorndike (1898), that primates are alone among nonhuman animals in being capable of 'non-vocal' or 'motor' imitation (Byrne, in press; Whiten and Ham, 1992). First, a number of studies have discredited the primary evidence of imitation in primates by showing that locale-specific behaviours, such as potato washing by Japanese macaques, *Macaca fuscata*, (Kawai, 1965; Itani and Nishimura, 1973) and termite fishing by chimpanzees, *Pan troglodytes*, (Goodall, 1986), are likely to have been acquired, not through imitation, but through individual, trial and error learning and/or non-imitative social learning. For example, Visalberghi and Fragaszy (1990a) reported that capuchin monkeys, *Cebus apella*, swiftly learned through their own efforts to wash food items when offered sandy food in the presence of water; and Teleki (1974) found that he was unable to fish effectively for termites despite months of careful observation of Gombe chimpanzees termite fishing (Galef, 1992). All recent reviews of the relevant literature have concluded that there is no unequivocal, experimental evidence of imitation in non-human primates (Galef, 1988, 1992; Tomasello, 1990; Visalberghi and Fragaszy, 1990b; Whiten and Ham, 1992). The assumption that monkeys and apes can 'ape' currently rests exclusively on observational, or anecdotal, evidence.

Second, experiments with budgerigars (*Melopsittacus undulatus*) (Galef et al., 1986) and rats (Heyes and Dawson, 1990; Heyes et al., 1992, 1993) have indicated that members of these non-primate species may be capable of imitation. Galef et al. (1986) gave budgerigars a series of trials in which each bird observed a conspecific using either its beak or its feet to remove a flat cover from the top of a food cup, and was then allowed to remove a similar cover itself. On the first two trials, the observer birds tended to use the same appendage as had their demonstrator to remove the cover, but performance on subsequent trials provided no evidence of demonstrator-consistent responding. Thus, Galef et al. (1986) reported a transitory imitation effect.

In their experiment with rats, Heyes and Dawson (1990) used a 'bidirectional control' procedure; a type of 'pattern control' (Galef, 1988), 'cross-target' procedure (Meltzoff 1988) or 'two-action test' (Whiten and Ham, 1992). During the initial phase of the procedure, each observer rat faced its conspecific demonstrator with a single manipulandum, a joystick, suspended vertically between them. The observers had been magazine trained, but they had not previously encountered the joystick. In accordance with prior, conventional instrumental training, the demonstrator pushed the joystick 50 times to the right or to the left of the observer's visual field, and each response was followed immediately by a tone and delivery of food to the demonstrator. 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. On test, the observer rats showed a significant tendency to push the joystick in the same direction relative to their own bodies as had their demonstrators.

Since 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 response learning by observation, or imitation, was responsible for the observed bias in directionality of responding. However, it is possible that the rats' test performance was an example of 'local enhancement' (Thorpe, 1956) or, more specifically, that it was influenced, instead or in addition to response learning, by stimulus-reinforcer associations learned during observation. For observers of 'left-pushing', for example, the movement of the joystick toward the front of the operant chamber signalled the delivery of food to the demonstrator and the sound of a tone that had accompanied delivery of food to the observer during magazine training. Consequently, the sight of the joystick moving towards the front of the chamber may have acquired reinforcing properties for the observers of left pushing, and this may have been responsible for their subsequent tendency to push it more to the left/front than did observers of right pushing. Thus, the observer rats' cue may have been the movement of the joystick effected by the demonstrators' behaviour, and not the behaviour itself.

The results of an experiment in which observational discrimination training occurred in the absence of conspecific demonstrators (Denny et al., 1988) lend weight to this hypothesis. Prior to being given access to a joystick manipulandum, the rats in this study observed the joystick moving automatically (without the intervention of a demonstrator) 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−), while 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 which Denny et al. (1988) attributed to 'purposeful' action following stimulus-reinforcer contingency learning.

The present experiments investigated the possibility, raised by Denny et al.'s (1988) findings, that stimulus-reinforcer learning, rather than imitation or response learning by observation, is responsible for the bias in responding observed in the bidirectional control procedure.

Experiment 1

Prior to their first contact with a joystick, the rats in Experiment 1 observed the joystick moving automatically (group AUTOMATIC) or manually (group MANUAL), i.e. through the action of a conspecific demonstrator. Half of the animals in each group observed the joystick moving to the left, and the other half observed it moving to the right. Following Heyes and Dawson (1990), it was anticipated that, on test, the members of group MANUAL would tend to push the joystick in the direction in which they had observed it moving. If stimulus-reinforcer learning was responsible for this effect, then one would expect a similar effect to be apparent in group AUTOMATIC. If, on the other hand, the biased responding of group MANUAL was due to response learning by observation, then one would not expect the rats in group AUTOMATIC to show any systematic bias in directionality of responding.

Method

Subjects

Forty experimentally naive, male, hooded Lister rats, obtained from Charles Rivers (UK) were approximately 4 months old when they served as subjects. Eight of these rats were demonstrators, and the remaining 32 were observers. They were housed in groups of five (one demonstrator and four observers) in moulded plastic and metal hanging cages (54 × 32 × 21 cm), with free access to water. The rats were maintained at 85% of their free feeding body weight throughout the experiment.

Apparatus

The animals were trained and tested in four identical operant chambers, each measuring 50 × 25 × 20 cm. The walls were made of sheet metal, the ceiling of clear Perspex, and the floor was of 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 alloy joystick (0.6 cm in diameter) was suspended from the ceiling, half way between the side walls. The free end of the joystick, which was 6.5 cm above the floor when the joystick was in a vertical position, could only be moved to the left or to the right in a plane parallel to that of the partition. The joystick was separated from the partition by a distance of 4 cm. This distance was 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 joystick during observation training.

Movement of the joystick by the demonstrators and observers was recorded via a low torque potentiometer pivot at the top of the joystick, above the roof of the chamber containing the animals. A constant voltage was applied across the pivot. Movement of the joystick by a rat resulted in rotation of a brush within the potentiometer, and hence to a voltage proportional to the degree of joystick displacement becoming available at the brush terminal. This DC potential was converted to a digital signal read by a BBC Master computer running Spider on-line control language. Automatic movement of the joystick was achieved by a solenoid at the top of the manipulandum with voltage adjusted such that the free end of the joystick was displaced 7.5 cm from its vertical starting position. When being observed, demonstrators also had to achieve a 7.5 cm displacement in order to register a response, but when observers were being tested the necessary displacement was 4 cm. After both automatic and manual displacement, the joystick was assisted back to a vertical position by a weight and a spring resting on the pivot of the manipulandum.

In addition to the joystick, the demonstration/test compartment contained a food tray situated at floor level in the middle of the wall opposite the partition. The food tray was illuminated on the inside by a 24 V, 2.8 W bulb, and entries to the tray were recorded via a photocell beam. Whenever a subject made a correct response (variously defined below), and whenever the joystick moved automatically in a direction designated correct, a 45 mg food pellet of mixed composition was automatically delivered to the food tray. Operation of the magazine was accompanied by the delivery of a 1000 Hz, 90 dB tone of 0.1 s duration from a loudspeaker directly above the food tray, extinguishing of the house light, and illumination of the tray light. The house light was switched on, and the tray light was switched off, 5 s later, or, if a tray entry was made within 5 s, when the next tray entry was registered. Following the delivery of a food pellet, the animal had to enter the tray before another reinforcer became available.

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.

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 7.5 cm or more were rewarded. At the end of training, all demonstrators showed perfect discrimination.

Initially all observers received four daily sessions of magazine training in the demonstration/test compartment from which the joystick had been removed. Thirty food pellets were delivered on a Random Time 45-s 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 joystick was moved, automatically or manually, to the left or to the right, 50 times. Each correct joystick movement was immediately followed by operation of the magazine, the sounding or a tone, and a change in illumination (see Apparatus). The observers consisted of pairs, with one member in group MANUAL and the other in group AUTOMATIC. The first member of each pair observed a demonstrator pushing the joystick to the left or to the right, and the second observed the joystick moving automatically in the same direction and with the same sequence of inter-movement intervals. That is, when a demonstrator performed for the first member of a pair, its sequence of inter-response times was recorded and used to control the automatic joystick movements to which the second member was exposed. When 50 joystick movements had occurred, the demonstrator (group MANUAL) or surplus food pellets (group AUTOMATIC) were removed from the apparatus, and the observer was immediately transferred to the demonstration/test compartment where joystick displacements of 4 cm or more in either direction were rewarded by the delivery of food. This test phase ended when the observer had made a total of 50 reinforced responses.

Results and Discussion

All demonstrators showed perfect discrimination while being observed. The demonstrators had a mean response rate of 7.12 (S.D. = 1.79, $n = 16$) per min, and therefore observers in both group MANUAL and group AUTOMATIC were exposed to joystick movements with a mean inter-movement interval of 8.43 s.

The test performance of each observer rat was classed as either observation-consistent or observation-inconsistent according to whether it made more or less than half of its 50 reinforced responses in the direction observed. Measured in this way, 12 of the 16 observers in group MANUAL ($Z = 1.75$, $P = 0.04$, 1-tailed), and only 8 of the 16 observers in group AUTOMATIC ($Z = 0$, $P = 0.50$) showed observation-consistent responding. Similar results were obtained when the observer rats were categorised on the basis of their initial test performance. Fourteen of the 16 rats in group MANUAL ($Z = 2.75$, $P = 0.003$, 1-tailed), and 9 of the 16 rats in group AUTOMATIC ($Z = 0.25$, $P = 0.40$), made their first reinforced response in the direction observed.

Experiment 2

In Experiment 1, rats that had observed the joystick being moved by a demonstrator tended to push it in the direction in which they had seen it move, while observers of automatic joystick movement showed no consistent directional preference. This suggests that the directional preferences of rats that observed demonstrator action were mediated by response learning by observation. However, another interpretation is possible. In group MANUAL, learning of a stimulus-reinforcer relationship may have been enhanced by the mere presence of a conspecific in the joystick compartment during the observation phase, or by that animal's consummatory behaviour. Thus, rather than having been influenced by the demonstrators' joystick-pushing behaviour, subjects in group MANUAL may have paid more attention to the moving joystick because a conspecific was nearby, or the demonstrators' consumption of the food delivered during observation may have enhanced the reinforcing properties of food delivery for the observers.

This hypothesis is weakened by evidence that vicarious reinforcement is not important with respect to stimulus-reinforcer learning in rats (Groesbeck and Duerfeldt, 1971; Kohn and Dennis 1972), and that the presence of a conspecific during observational discrimination training can retard subsequent performance (Robertson et al., 1985). However, the hypothesis was tested in Experiment 2 by exposing rats to automatic joystick movement with a passive, hungry conspecific (a 'collector') in the joystick compartment. If this procedure were to result in observation-consistent responding, it would suggest that stimulus-reinforcer learning is indeed sufficient to account for the directional preferences of rats that have observed a demonstrator pushing the joystick.

Method

Subjects

Thirty experimentally naive, male, hooded Lister rats, obtained from Charles Rivers (UK) were approximately 6 months old when they served as subjects. Ten of these were collectors, and the remaining 20 were observers. They were held in groups of three (one collector and two observers). All other housing and feeding conditions were the same as those of Experiment 1.

Apparatus and procedure

The apparatus and procedure were identical to those described in Experiment 1 (group AUTOMATIC) except in the following respects.

To ensure that they would collect food pellets from the tray promptly while being observed, each collector was placed in the joystick compartment for four, daily sessions in which they received 50 food pellets each signalled by a joystick movement. Five of the collectors had food delivery signalled by movement of the joystick to the right, and the other five by movement to the left. The sequence of intertrial intervals was different in each session, and was controlled by a recording, made during Experiment 1, of a demonstrator's sequence of inter-response times.

A collector was present in the joystick compartment while each observer was exposed to 50 automatic movements of the joystick, with each movement immediately followed by a tone and magazine operation. Half of the rats observed left movement and were accompanied by collectors that had been trained with left movement signalling food delivery, and vice versa for rats that observed right movement. Each observer was exposed to a different sequence of inter-movement intervals, matched to an inter-response interval sequence generated by one of the demonstrators in Experiment 1. The mean inter-movement interval was 5.46 s (S.D. = 0.95).

Results and Discussion

On test, two subjects failed to obtain 50 reinforcers within 1 h, and were therefore excluded from the analysis.

On average, collectors entered the food tray 1.69 s (S.D. = 0.49) after pellet delivery was initiated. These figures, and informal observations, suggested that, while the collectors remained close to the tray throughout the period in which they were observed, they did not sit with their heads inside the tray opening between pellet deliveries.

The test performance of each observer rat was classified as either observation-consistent or observation-inconsistent, as in Experiment 1. Nine of the 18 observers made more than half of their 50 reinforced responses in the direction observed ($Z = 0$, $P = 0.50$), and 12 of the 18 observers made their first test response in the direction observed ($Z = 1.18$, $P = 0.12$). Thus, as a group, the rats in this experiment did not show an observation-consistent response bias.

A combined analysis of the data from Experiments 1 and 2 confirmed that more observation-consistent responding occurred after observers saw a demonstrator moving the joystick. Twelve of the 16 observers in group MANUAL (Experiment 1), and only 17 of the 34 rats that saw automatic joystick movement (Experiment 1, group AUTOMATIC, plus Experiment 2), made more than 50% of their responses in the observation-consistent direction ($Z = 1.65$, $P = 0.05$, 1-tailed).

General Discussion

Experiments 1 and 2 showed that rats which have observed a conspecific demonstrator pushing a joystick to the left or to the right tend to push it in the same direction, while rats that have observed a joystick moving to the left or right automatically, in the presence or absence of a conspecific, do not exhibit a response bias consistent with their observation experience. The absence of an observation-consistent response bias in observers of automatic joystick movement suggests that the bias exhibited by observers of demonstrator action is due, not to stimulus-reinforcer learning, but to response learning by observation, i.e. observational learning or imitation.

Denny et al. (1988) found that observation of automatic joystick movement affected the direction of rats' subsequent responses, while Experiments 1 and 2 found no such effect. This is not surprising given that the present procedures differed from those used by Denny et al. (1988) in a number of respects. For example, in the Denny et al. study: the rats were pretrained to orient their bodies toward the joystick; joystick movements signalled delivery of food to the observer; and each subject was exposed to as many as a 1000 joystick movements, to both left and right, with movements in only one direction signalling reinforcement. The results of a simultaneous, visual discrimination experiment with pigeons (Biederman and Vanayan, 1988) suggest that the latter variable, provision of explicit discrimination training, may have been important with respect to Denny et al.'s positive outcome. Biederman and Vanayan (1988) tested pigeons on an inverted triangle (S +) vs. erect triangle (S −) discrimination after observation experience consisting predominantly of S + trials (the flashing of an inverted triangle signalled the delivery of inaccessible grain), or of a mixture of S + and S − trials (an erect triangle flashed and the trial terminated). The performance of the latter, mixed trial group was superior, suggesting that exposure to both stimulus-reinforcer and stimulus-no reinforcer relationships facilitates this kind of observational discrimination learning.

In providing evidence of a different kind of observational discrimination learning in rats, an imitative variety involving response learning by observation, the results of Experiments 1 and 2 are consistent with those of another study using the bidirectional control procedure. In that experiment (Heyes et al., 1992) half of the observer rats were trained and tested in the same way as group MANUAL in Experiment 1. For the other half, the location of the joystick was changed between observation and testing, and its axis of movement was rotated through 90°. As a result, the joystick moved toward a different location in space when these animals observed a demonstrator making a left response, and when they made a left response themselves on test. In spite of this transformation, both groups of rats tended to push the joystick in the same direction, relative to their own bodies, as had their demonstrators. Like the results of the present study, this effect cannot readily be explained in terms of 'local enhancement' or stimulus-reinforcer learning.

Thorndike (1898) suggested that primates can, and other nonhuman animals cannot, imitate. In providing evidence that rats can imitate, the bidirectional control procedure has contributed to undermining this position. It seems most unlikely that the inverse of Thorndike's hypothesis is true, but there remains a question as to whether the current lack

References

Biederman, G.B. and Vanayan, M., 1988. Observational learning in pigeons: The function of quality of observed performance in simultaneous discrimination. Learn. Motiv., 19: 31–43.

Byrne, R.W. (in press) The evolution of intelligence. In: P.J.B. Slater and T.R. Halliday (Editors), Behaviour and Evolution, Cambridge University Press, Cambridge.

Cook, M., Mineka, S., Wolkenstein, B. and Laitsch, K., 1985. Observational conditioning of snake fear in unrelated rhesus monkeys. J. Abnormal Psychol., 93: 355–372.

Denny, M.R., Clos, C.F. and Bell, R.C., 1988. Learning in the rat of a choice response by observation of S-S contingencies. In: T.R. Zentall and B.G. Galef (Editors), Social Learning: Psychological and Biological Perspectives, Erlbaum, Hillsdale NJ, pp. 207–223.

Galef, B.G., 1988. Imitation in animals: History, definition and interpretation of data from the psychological laboratory. In: T.R. Zentall and B.G. Galef (Editors), Social Learning: Psychological and Biological Perspectives, Erlbaum, Hillsdale NJ, pp. 3–28.

Galef, B.G., 1992. The question of animal culture. Human Nature, 3: 157–178.

Galef, B.G., Manzig, L.A. and Field, R.M., 1986. Imitation learning in budgerigars: Dawson and Foss 1965 revisited. Behav. Process., 13: 191–202.

Galef, B.G. and Stein, M., 1985. Demonstrator influence on observer diet preference: Analyses of critical social interaction and olfactory signals. Anim. Learn. Behav., 13: 31–38.

Goodall, J., 1986. The Chimpanzees of Gombe. Harvard University Press, Cambridge.

Groesbeck, R.W. and Duerfeldt, P.H., 1971. Some relevant variables in observational learning of the rat. Psychonom. Sci., 22: 41–43.

Hall, K.R.L., 1963. Observational learning in monkeys and apes. Br. J. Psychol., 54: 201–226.

Heyes, C.M., 1993. Imitation, culture and cognition. Anim. Behav., 46: 999–1010.

Heyes, C.M., 1994. Social learning in animals: Categories and mechanisms. Biological Rev.

Heyes, C.M. and Dawson, G.R., 1990. A demonstration of observational learning using a bidirectional control. Quart. J. Exp. Psychol., 42B: 59–71.

Heyes, C.M., Dawson, G.R. and Nokes, T., 1992. Imitation in rats: Initial responding and transfer evidence. Quart. J. Exp. Psychol., 45B: 229–240.

Heyes, C.M., Jaldow, E. and Dawson, G.R., 1993. Observational extinction: Observation of nonreinforced responding reduces resistance to extinction in rats. Anim. Learn. Behav., 21: 221–225.

Itani, J. and Nishimura, A., 1973. The study of infrahuman culture in Japan. In: W. Montagna (Editor), Symposium of the Fourth International Congress of Primatology, Precultural Primate Behavior, Karger, Basel, pp. 26–50.

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

Kohn, B. and Dennis, M., 1972. Observation and discrimination learning in the rat: specific and nonspecific effects. J. Comp. Physiol. Psychol., 78: 292–296.

Mackintosh, N.J., 1983. Conditioning and Associative Learning. Clarendon Press, Oxford.

Meltzoff, A.N., 1988. Imitation, objects, tools, and the rudiments of language in human ontogeny. Human Evol., 3: 45–64.

Morgan, C.L., 1900. Animal Behaviour. Edward Arnold, London.

Petrinovich, L., 1988. The role of social factors in White-Crowned sparrow song development. In: T.R. Zentall and B.G. Gales (Editors), Social Learning: Psychological and Biological Perspectives (ed.), pp. 255–278. Erlbaum, Hillsdale NJ.

Robertson, H.A., Vanayan, M. and Biederman, G.B., 1985. Observational learning and the role of confinement in pigeons: Suppression of learning as a function of observing the performance of a conspecific. J. Gen. Psychol., 112: 375–382.

Teleki, G., 1974. Chimpanzee subsistence technology: Materials and skills. Human Evolution., 3: 575.

Thorndike, E.L., 1898. Animal Intelligence. Psychol. Rev. Monographs, 2: No. 8.

Thorpe, W.H., 1956. Learning and Instinct in Animals. Methuen, London.

Tomasello, M., 1990. Cultural transmission in the tool use and communicatory signalling of chimpanzees? In: S. Parker and K. Gibson (Editors), Language and Intelligence in Monkeys and Apes, Cambridge University Press, Cambridge, pp. 274–311.

Visalberghi, E. and Fragaszy, D.M., 1990a. Food washing behaviour in tufted capuchin monkeys and crabeating macaques. Anim. Behav., 40: 829–836.

Visalberghi, E. and Fragaszy, D.M., 1990b. Do monkeys ape? In: S. Parker and K. Gibson (Editors), Language and Intelligence in Monkeys and Apes, Cambridge University Press, New York, pp. 247–273.

Whiten, A. and Ham, R., 1992. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In: P.J.B. Slater, J.S. Rosenblatt, C. Beer and M. Milinski (Editors), Advances in the Study of Behavior, Vol. 21, Academic Press, New York.

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