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Push or pull: an experimental study on imitation in marmosets

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Abstract. A laboratory experiment was conducted in order to explore the possibility of imitation, that is, response learning by observation, in marmosets, *Callithrix jacchus*. Inexperienced individuals were allowed to observe a skilful model that demonstrated one of two possible techniques (pushing or pulling a pendulum-door) to get food from inside a wooden box. Their initial manipulative actions, performed when exposed to the box in a subsequent test, were compared with those of naive control subjects (non-observers). The observers showed less exploratory behaviour than the non-observers and, more importantly, some showed a strong tendency to use the demonstrated opening technique in the initial test phase. This initial preference disappeared in the course of five test sessions and the observers converged towards the simpler, alternative solution that was generally preferred by the non-observers. Despite fundamental individual differences in the observer group and the failure to find a significant group effect, the results indicate that marmosets are capable of learning simple motor skills through conspecific observation.

The basic tenet of the social ('Machiavellian') intelligence hypothesis is that, although most research has focused on how intelligence deals with the physical or technical world, intelligence emerged as a response to dealing with other individuals (Whiten & Byrne 1988). One reason why the social world might be so challenging is because the problems are not related to physical objects or events, but to other individuals, which are themselves reactive. Clearly, dealing with other members of a social group requires a constant monitoring of their states, within a range from behavioural events to mental ones. We may conclude from this that, if 'the chief role of creative intellect is to hold society together' (Humphrey 1988, page 18), natural selection should have strengthened the aptitude for mutual observation in social species.

The scientific inquiry becomes particularly interesting if information from both domains, the social and the technical, co-occur. The functional value of inter-individual observation might have been increased by the ability to exploit knowledge about others and to benefit from the discoveries of others through social learning. Whether an animal learns about stimuli, objects or events in the environment (non-imitative social learning), or about responses, actions, or behaviour patterns (imitative social learning), the functional value as a means of producing behavioural co-ordination among members of a group has been broadly acknowledged (Visalberghi & Fragaszy 1990). However, although evidence for the functional significance of the various kinds of observational learning has been provided, almost 100 years of research on this topic have failed to distinguish imitative and non-imitative versions clearly (Galef 1988).

In recent years, three main types of social learning have been crystallized from a vast array of phenomena: (1) social facilitation (Zajonc 1965); (2) local (Thorpe 1956) and stimulus enhancement (Spence 1937); and (3) imitation (Thorndike 1898; Morgan 1900; Thorpe 1956). The first refers to a motivational facilitation of performing a behavioural act already in the individual's repertoire (whether acquired phylogenetically or ontogenetically), through experiencing another individual behaving similarly. The second phenomenon denotes a conspecific eliciting a

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movement towards a novel place or object by directing the attention of an observer to some salient feature in the environment. In both cases of non-imitative social learning, as well as in the following imitative one, the production of similar behaviours among members of a group is caused by the transmission of information about the environment and even about behaviour through conspecific observation (subsumed under the term 'observational learning', Hall 1963). However, while in the first two cases the receiver animal must not only observe the transmitter animal, but also act on its environment, in order to shape the proficient behaviour, 'true' imitation provides a means of copying a behaviour and learning about its consequences through observation alone (Heyes 1993).

Reports of imitation-like behaviour are known from observational studies of animal behaviour, for example Romanes (1883), as well as from the beginnings of experimental psychology, for example Thorndike (1898). The range of species experimentally investigated since then includes octopuses, *Octopus vulgaris*, several bird species such as tits, *Parus* spp., red-winged blackbirds, *Agelaius phoeniceus*, budgerigars, *Melopsittacus undulatus*, and pigeons, *Columba livia*, but only a few non-primate mammals such as rats, *Rattus norvegicus*, dolphins, *Tursiops aduncus*, sea otters, *Enhydra lutris*, and dogs, *Canis familiaris*; for a review see Zentall & Galef (1988), Whiten & Ham (1992), Heyes & Galef (1996). Evidence of observational learning in primates is primarily provided from a wealth of field studies; for a review see Hall (1963), Visalberghi & Fragaszy (1990), Moore (1992) and Byrne (1995). These reports from the wild, along with the few laboratory studies that were conducted to demonstrate imitation, have failed, however, to provide a clear answer to the question of which of the investigated species is able to perform the full range of observational techniques.

Our primary purpose in the present experiment was to examine whether monkeys, in addition to rats (Heyes 1995) and apes (Byrne & Tomasello 1995; Whiten et al. 1996), are able to learn through imitation. Our attempt is based on our doubts about the assumption that these species can, and monkeys cannot, imitate. Only recently, Visalberghi & Fragaszy (1960) argued convincingly that the limitations of imitation are confined to tool use and other technical problems, which play a subordinate role in the wild. Although Hauser (1988) reported imitation-like behaviour in vervet monkeys, *Cercopithecus aethiops*, that dip leaves into exudate from a tree, and Chevalier-Skolnikoff (1989) reported seeing 32 examples of imitative learning in several species of New World monkeys, *Ateles* sp., *Cebus* spp., all such anecdotes have been questioned and simpler explanations have been offered. Recent reviews of the monkey literature finish with the pessimistic assertion that imitation remains to be proved (Whiten & Ham 1992) or is at best a fragile phenomenon in animals that were popularly labelled as 'born mimics' (Fragaszy & Visalberghi 1989; Moore 1992).

We used common marmosets, *Callithrix jacchus*, as experimental subjects. Using the observational learning paradigm, we first allowed them to observe individually a trained model solving a technical problem, and subsequently tested them to determine whether exposure to the model resulted in actions that initially matched those of the skilful demonstrator. By employing the 'two-action' procedure (Dawson & Foss 1965) in which the task can be solved by two responses rather than a single one, that is, pushing or pulling a pendulum-door in order to gain access to food inside a box, we provide a detailed analysis of the parameters required for claiming imitation, rather than merely demonstrating the ability of animals to benefit from exposure to the model.

Moreover, in addition to the commonly used 'non-exposed control' (Heyes et al. 1992) or 'savings' (Moore 1992) method that requires comparing the learning rates of groups that have or have not observed a model performing some target response, the present procedure involves aspects of controlling for non-imitative effects. We control for facilitation effects by requiring the observers to wait before being tested in the absence of the demonstrator ('delayed condition', Huang et al. 1983). To control for enhancement effects, that is, that the model's behaviour has merely attracted the observers' attention to a particular part of the test environment, we applied one aspect of the 'pattern control' procedure, a variant of the two-action method devised by Heyes and co-workers in the rat laboratory (Heyes & Dawson 1990; Heyes et al. 1992). By requiring the model only to pull the door, but allowing the observer animals to try both pulling and pushing when tested, we could determine the probability of true imitation from the initial proportion of the frequencies of both actions. Although we have not used a control group observing the alternative response, as required by the pattern-control procedure, we tried to control for enhancement effects by investigating the pattern of initial manipulation of the pendulum-door. A detailed analysis of the way the observers initially manipulated the door can help to elucidate whether they have really copied the demonstrated behaviour or were only motivated to pay attention to the apparatus and to manipulate it by using their own techniques (Byrne & Tomasello 1995).

METHODS

Subjects

We used 18 individuals as experimental subjects. At the time of the study they were held in two groups at two locations in Vienna. The Institute of Zoology at the University of Vienna housed eight captive-born adult individuals (three males, five females), all brothers and sisters with no exclusive pair bondings. This group was kept in an indoor–outdoor cage of welded mesh (each cage measuring 250 × 250 × 250 cm) equipped with several branches and living plants. In the Institute of Laboratory Animal Science at the University of Veterinary Medicine 10 individuals were kept in pairs (three male–female pairs, one male–male pair) or solitary (two males) in laboratory cages (50 × 50 × 70 cm). In most cases, two cages were connected. All were equipped with twigs and a small pendulum-plate.

All animals were fed on a fixed diet of fruit with protein and vitamin supplements and maintained under the general conditions recommended for marmosets in captivity (Moore 1989). The animals were kept at a temperature of 26–28°C during the day and 21–23°C at night and a humidity of 75%. Daylight was the main source of lighting in the Institute of Zoology and artificial light the main source of lighting in the Institute of Laboratory Animal Science.

Apparatus

The apparatus consisted of a wooden box (20 × 10 × 10 cm) with a single pendulum-door, hinged at the roof, replacing one of the small side walls (Fig. 1a). To get banana pieces (50 pieces with a total weight of 30 g) from inside the box the monkeys had to open the door by either pushing or pulling. The model/observer studies took place in an experimental cage (125 × 70 × 260 cm) to which the monkeys had access through a passageway from the adjacent but visually isolated indoor cage (Fig. 1b). The experimental cage was divided into three compartments, an observation chamber (40 × 70 × 145 cm), a manipulation chamber (85 × 70 × 145 cm) and a waiting chamber (80 × 70 × 115 cm). All chambers were connected by a passageway with several guillotine

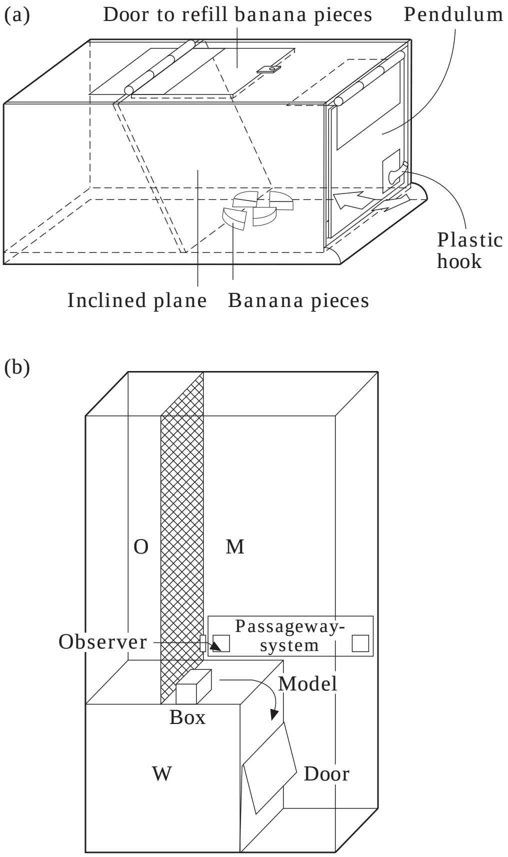

Figure 1. (a) Diagram of the apparatus showing the pendulum-door in the front of the wooden box and indicating the position of the banana pieces inside the box; (b) diagram of the experimental situation showing the relationship between the three compartments: O: observation chamber, M: manipulation chamber, W: waiting chamber.

doors. The apparatus was put on the opaque platform of the manipulation chamber in a position 10 cm away from the wire mesh separating the observation chamber.

Procedure

Only the marmosets at the Institute of Zoology were used as models or observers. Before the experiment started the monkeys were familiar with both the experimental set-up and the use of the passageways. During the testing phase all monkeys were fed their daily diet, except bananas.

We selected one male (JU) of middle rank to serve as a model in the following demonstration sessions. Rank was determined by feeding protocols taken during 15 days before and 10 days after the experiments. In marmosets, male and female subjects are in separate rank hierarchies, and particularly in our group the males are above the females. Subject JU was the lowest ranking male but of middle rank in the whole group (above the five females). He was first trained to solve the task of opening the box solely by pulling. His tendency to push was prevented by a small nail stopper inside the box behind the pendulum-door. Training was continued until he performed in a skilled and consistent manner.

We used the seven remaining subjects as observers. They were all trained and tested individually. At the beginning of an observation session we let an observer subject into the observation chamber and put the model into the manipulation chamber with free access to the banana box. Immediately after the model had finished eating 15 g of banana pieces he was transferred to the waiting chamber and the observer was allowed to enter the manipulation chamber. These opportunities to enter the manipulation chamber were provided in order to familiarize the observer animals with the context in which the tests would later be conducted. However, we removed the apparatus so that the subjects could not touch it before the onset of the test phase. The observation phase consisted of one session on each of 3 consecutive days. The test phase began immediately after the third observation session and consisted of one session on each of 5 consecutive days. In these sessions the observers had free access to the banana box and could open the pendulum-door by either pushing or pulling. We gave subjects unlimited time to solve the problem (a post hoc analysis revealed an average session length of 6 min). The sessions were terminated by the consumption of the bananas.

We carried out control studies with the 10 subjects of the second group of marmosets. Unlike the experimental situation described above, the subjects were trained individually in visually isolated laboratory cages. In these studies the animals were confronted with the opening problem in 20-min sessions on 5 consecutive days. Without previous exposure to a proficient conspecific they were required to explore the box and manipulate the pendulum-door in order to get the desired banana pieces.

All sessions were videotaped in their entirety. We classified the behaviour at the apparatus according to (1) three types of object exploration, namely sniffing, gently biting and touching the apparatus; and (2) two categories of object manipulation, namely the modality (push or pull) and the effectiveness (success) of opening. During the observation phase we also measured the relative distance between model and observer, the frequency and duration of monitoring the model and its actions, and every type of model–observer interaction. From the detailed analyses of the test results, two out of seven observers had to be omitted because of an initial technical problem with the pendulum-door (the door was locked because of a defective hinge).

RESULTS

Observation Phase

The observation session lasted for 2.5 ± 0.5 min ($\bar{X} \pm$ SD). During this time the model pulled the pendulum-door 19 ± 4.35 times ($\bar{X} \pm$ SD) by predominantly using his left hand (76%). He was rewarded with banana pieces in $72 \pm 7.91\%$ of completed trials ($\bar{X} \pm$ SD). The presence of an observer influenced the behaviour of the model in two different ways. The efficiency (success rate) of pulling declined from the mean value when the observers were males (two-way ANOVA: $F_{6,14}=3.232$, $P<0.05$; and multiple mean comparison by Student–Newman–Keuls: $P<0.05$), whereas agonistic displays were shown only when observers were females. Although aggressive interactions were rare (median = 1 per session) the model directed his encounters especially against

Figure 2. A sketch of a pair of monkeys involved in a demonstration/observation event.

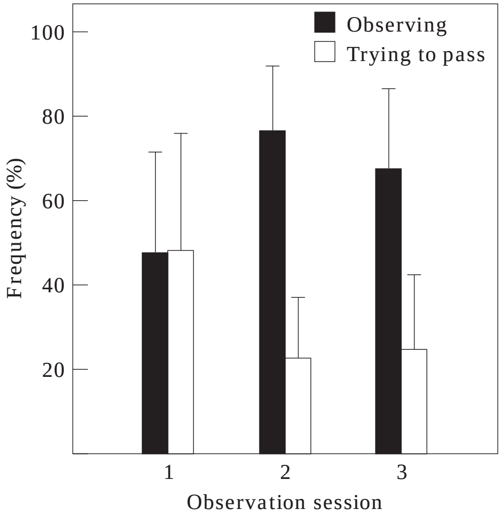

Figure 3. The relative frequencies of observing the demonstrator and of attempting to get into the adjacent chamber are depicted as a mean of all five observers during three sessions of observation.

two subjects: GO was the partner in 13%, STI in 85% of the encounters.

All observers were attracted by the model. They observed his actions frequently, mostly sitting in a position next to the wire mesh near the box (Fig. 2). The frequency and duration of observing the pulling activities were similar between the subjects but were distributed differentially over the three demonstration sessions (Fig. 3). On day 1, the monkeys watched (fixed the model binocularly) about 50% of the pulling actions of the model; when not watching the pulling actions of the model they usually tried to get into the adjacent chamber. These attempts decreased on day 2, while the number of observed actions increased significantly (two-way ANOVA: $F_{2,18}=4.047$, $P<0.05$; and multiple mean comparison by Bonferroni: $P<0.05$). On day 3, the number of observed actions was still very high, but did not differ significantly from day 1 and 2.

During the observation phase the monkeys were also attracted by pieces of banana that were occasionally dropped by the model ($\bar{X} \pm$ SD per session $=3 \pm 3.08$; minimum $=0$, maximum $=10$). All observers tried to get these pieces immediately, but they were successful in only $47 \pm 25.14\%$ of their trials ($\bar{X} \pm$ SD). We conducted two general linear models in order to investigate possible effects of scrounging. The first used the rate of observed pulling actions of the model as the dependent variable and the second the duration of observation. In both analyses six factors were used as predictor variables, namely (1) the model's success, (2) the number of interactions between model and observer, (3) the number of scrounging opportunities, (4) the success of scrounging, (5) the dominance rank of the observer, and (6) the position in the sequence in which the observer was tested. There was no significant effect of the observation rate or the duration of observation (observation rate: $F_{6,14}=2.584$, NS; observation duration: $F_{6,14}=1.967$, NS).

Test Phase

When observers were allowed to approach the test apparatus they immediately directed their attention towards the pendulum-door. First, they showed a short bout of exploration that consisted predominantly of olfactory, in contrast to tactile, activities ($\bar{X} \pm \text{SD} = 5 \pm 2.17$ explorations/min; Wilcoxon signed-ranks test: $T=-2.121$, $N=5$, $P<0.05$; Fig. 4). In manipulating the door, three out of five observers (CS, SU, GO) used pulling from the beginning (Table I). CS and SU acted in a manner very similar to the model. Like JU they inserted the claws of the left hand in the right lateral gap between the pendulum-door and the frame of the box or at the hook (Table II). They pulled the door with the left hand and held it in an open position while they used the right hand to grab for banana pieces. Both subjects predominantly performed this pulling behaviour for the

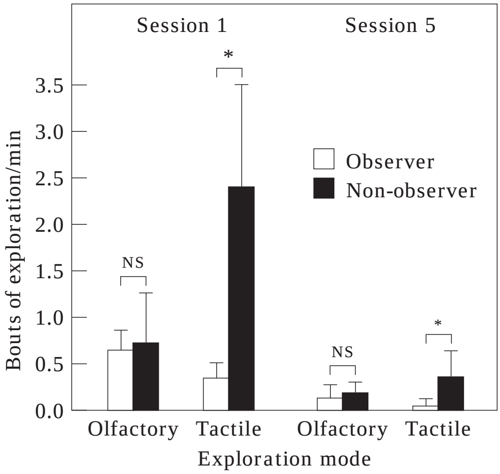

Figure 4. A comparison of the exploratory behaviour (number of olfactory and tactile explorations per min) between observer and non-observer animals in the first and the fifth test session.

whole first session. CS first pushed the door after a series of 25 pulling actions, while in SU this behaviour occurred after a series of 12 pulling actions. The third subject that initially pulled (GO) used his own method (using the right hand and inserting the fingers in the crack between the door and the box in order to pull) and did so only four times before the first pushing. The remaining two subjects (LA, SH), however, started with pushing and continued to open the door in this manner while using their arms (LA) or head (SH). Regardless of whether they used pulling or pushing, all observers achieved success within the first minute, on average after six exploratory activities (±2.28 SD; minimum 3, maximum 8) and two manipulations of the pendulum-door (±2.12 SD; minimum 0, maximum 5). In further test sessions the monkeys did not improve their success in obtaining banana pieces (Wilcoxon signed-ranks test: $T=0.730$, $N=5$, NS). Nevertheless, all subjects who originally opened the door by pulling changed their preference to frequently pushing. The two subjects who started with pushing maintained this strategy (Table I). In contrast to the similarities between the actions of the model and CS and SU while pulling, each of the monkeys had a special technique in pushing, using one or both hands (more the left or the right), the arms and the head (Table II).

Like the observer subjects, naive control subjects approached the test apparatus immediately. However, within the first session the individuals differed markedly in the time they spent at the apparatus (from 2 to 12 min), and thus also in the frequency of exploration (minimum 21, maximum 117) and manipulation (minimum 5, maximum 158). Exploratory behaviour consisted mainly of tactile, in contrast to olfactory, components (Wilcoxon signed-ranks test: $T=2.201$, $N=6$, $P<0.05$; Fig. 4). After 34±18.37 ($\bar{X}\pm$ SD) exploratory activities these monkeys started to manipulate the pendulum-door by using both pulling and pushing (Table I). In the first 15 trials none of the subjects showed a series longer than three times in pulling and five times in pushing. Manipulation of the pendulum-door did not lead to immediate success. It took the subjects 63±28.79 exploratory acts ($\bar{X}\pm$ SD) and 31±2.99 manipulations to get the first piece of banana. Furthermore, almost all subjects of the control group got the reward only by pushing. Thus, at the end of the experiment all control subjects handled the pendulum-door predominantly by pushing ($\bar{X}\pm$ SD = 85±16.8%).

We used five general linear models to investigate the influence of several factors on the following dependent variables: (1) the number of exploratory bouts; (2) the number of manipulations; (3) the rate of pulling; (4) the efficiency (success) in pulling; and (5) the efficiency in pushing. The pulling rate was calculated as a discrimination ratio for each animal by dividing the number of pulls by the total number of manipulations made by the animal during a test session. The efficiency of a manipulation is given as the proportion of successful responses. In all models we investigated the effects of the following four predictor variables: previous experience (observers versus non-observers), individual differences, sex and session (Table III).

Except for the number of manipulations, we found for all response variables one or more factors that had an effect on their variance. First, the variance in the number of explorations can be explained by both previous experience and session. The frequency of exploration decreased in both groups in the course of the test phase but it was generally higher in the observer than the non-observer group.

Second, all of the variance of pulling success can be explained by previous experience,

Table I. Exploration and manipulation behaviour of the observers and control subjects during the first and the fifth sessions of testing

		Exploration		Manipulation				
	Subject	Olfactory	Tactile	Pull	Push	Pull:push %	Success in pulling %	Success in pushing %
	Model	—	—	19	—	100:0	72	—
Observers								
Session 1	CS	5	3	37	2	95:5	49	0
	SU	4	2	26	8	76:24	58	38
	GO	2	1	10	6	63:37	60	50
	LA	5	3	5	47	10:90	0	35
	SH	3	1	0	9	0:100	0	89
	Total	19	10	78	72			
Session 5	CS	1	0	6	34	15:85	33	56
	SU	0	0	9	15	38:67	67	25
	GO	0	0	15	25	38:62	30	100
	LA	0	0	1	17	6:94	100	46
	SH	2	1	10	18	36:64	20	67
	Total	3	1	41	109			
Controls								
Session 1	HE	6	57	11	40	22:78	0	38
	HA	14	56	16	9	64:36	0	0
	IV	9	49	3	2	60:40	0	0
	IR	5	16	3	3	50:50	0	0
	AA	34	83	18	140	11:89	0	9
	AL	18	26	0	7	0:100	0	0
	Total	86	287	51	201			
Session 5	HE	1	3	0	33	0:100	0	49
	HA	4	9	20	28	42:58	0	43
	IV	0	4	14	38	27:73	0	32
	IR	7	5	1	48	2:98	0	27
	AA	5	17	14	74	16:84	0	19
	AL	2	1	1	32	3:97	0	22
	Total	19	39	50	253			

The total numbers of olfactory and tactile exploration activities as well as the total numbers of pulls or pushes, their relative frequencies, and the relative success of these responses are shown. The corresponding data of the model are given as a mean of all activities.

indicating that the efficiency of pulling depends strongly on the possibility of having observed a model demonstrating pulling before. In contrast, the efficiency of pushing does not depend on previous experience but on the session which represents the course of testing. In fact, the success rate of pushing increased for all subjects with time.

Finally, a very high proportion of the variance in the pulling rate is caused by individual differences, only a small proportion by previous experience and session, and almost nothing by sex. This main effect of individual differences prevents us drawing firm conclusions about the effect of previous experience on the rate of pulling, because the interaction between individual and previous experience is very strong ($P<0.05$). Therefore, we added an additional analysis of the differences in pulling rate between groups.

Following the prediction of imitation theory that animals learn a response or a response-reinforcer relationship by observation, we should find a response bias in favour of the demonstrated response. Thus, according to the traditional test design of experimental psychology, the observer group should demonstrate a significantly higher proportion of pulling than the control group. This is not the case, whether we compare the two groups by counting their manipulations over the entire test phase (five sessions) or by counting only a variable number of initial manipulations. Although in any case the observers pulled at a higher rate than the non-observers, a Mann–Whitney U-test on pull rate reveals that this difference was not significant at an α-level of 0.05: whole first session, $U=11.5$, $N_1=5$, $N_2=6$, NS; the first four responses: $U=9.5$, $N_1=5$, $N_2=6$, NS; the first five responses: $U=10$, $N_1=5$, $N_2=6$, NS; the first 15 responses: $U=10.5$, $N_1=5$, $N_2=6$, NS. The primary reason for this failure to find a significant group effect is that only three out of five observers started off by using a pulling motion when they had access to the apparatus (CS, SU, GO). Although these three observers showed the highest pull rates of all animals, it was insufficient to yield a significant group difference. In this respect, our results did not meet the level of reliability for proposing true imitation behaviour that was recently set in the psychological laboratory (see Heyes & Dawson 1990; Heyes et al. 1992).

However, beyond only small quantitative differences between the two experimental groups regarding the proportion of pulling in the initial test phase, we found a striking qualitative difference. Not only were the subjects of the observer group significantly more successful in their attempts to get bananas out of the box, regardless of the opening technique (the mean success rate of the observer group in the first test session was 0.61 versus for the control group 0.046; $U=0$, $N_1=5$, $N_2=6$, $P<0.01$), but it is crucial to note that none of the control subjects ever succeeded by pulling. In sharp contrast, those observers who pulled from the onset were very successful. From the first 10 pulling attempts, SU acquired banana pieces seven times, GO six times, and CS five times. However, it is important to recognize that pulling in these subjects was not reinforced either in all or in the initial attempts (only in SU was the first pulling response reinforced, in GO the fourth, in CS the third). Therefore, the initial persistence of pulling by these three subjects cannot be easily explained by reinforcement alone.

To explain the crucial difference in success rate between the two groups it might be useful to analyse the pulling action in more detail. Pulling the pendulum-door in order to get food was not a simple, single motor act (see above). Instead it was a compound action-pattern composed from several independent and dependent parts. At the level of the shape of the total action, we have to consider different movements of body parts relative to each other, and at the level of the time structure of the action, a specific sequencing of a series of sub-actions within a structured whole. To estimate the probability of executing exactly the model's solution we found it most appropriate to calculate the combined probability of at least five occurrences. These are (1) to use the left hand, (2) to take the pendulum-door from the right-hand gap, (3) to pull, (4) to hold the door wide open while grasping, and (5) to get the food which is dependent on case (4). Because there might be some bias in how animals naturally approach such a task, we calculated the probability of each of the action elements from the non-observer's actions during their first session (the corresponding data are given in Table II). The relative frequency of using the left hand was 0.47, to grasp the pendulum-door from the right-hand gap was 0.31, to pull was 0.35, to hold the door wide open while grasping was 0.0, and to get food was also 0.0. To estimate reliably the probability of occurrence of this whole sequence it is appropriate to take the values of the upper 95% confidence limits instead of the original data (thus the values are 0.81, 0.73, 0.73, 0.41, 0.41). Although these latter values are considerably higher than the real ones (for the benefit of reliability) the probability of occurrence of the model's action pattern is rather low ($P=0.073$). Thus it is unlikely that such a combination of four independent cases and one dependent case occurs by chance. If one calculates the probability that such a behavioural sequence occurs (at least) in two observer subjects, the formula of the binomial distribution yields a value of $P=0.045$. This means that the conclusion that subjects CS and SU have indeed imitated rests on a firm basis.

DISCUSSION

In summary, we found some more or less strong differences in both factors that are important to compare the two experimental groups, that is, the exploratory behaviour and the solving of the technical problem. The comparison of the exploratory behaviour reveals a significant group difference. Observers not only explored very little, their activities were also restricted to olfactory exploration. This seems plausible if one considers that information from the latter modality, in contrast to the visual, was not accessible during observation.

If the experimental setting has produced true imitative behaviour in our callitrichid group, one expects to find a significant group difference in the tendency to perform the response that was demonstrated by the model. Such a general facilitating effect on the tendency to try the solution performed by the model was not found. Only some of the observer animals in the crucial initial phase of the test opened the door predominantly by pulling. A significant group difference in the number of attempts was not observed. Furthermore, even this initial pull tendency disappeared in these three observer animals. The simple reason for the latter was a total shift in the behaviour of the 'imitators' towards the seemingly simpler solution in the course of the test phase.

The most salient difference in the test behaviour of the two experimental groups was found with regard to the success rate of pulling. While we found no case in which a control animal acquired food by pulling, all three observers that were inclined to pull were successful in more than half of their attempts. This indicates not only that observation has positive effects on the solving of a technical problem, but implicitly that successful pulling of a pendulum-door does not solely emerge from the behavioural repertoire of the species. The strong asymmetry in the efficiency of the opening technique also allows us to conclude that pulling the door is not a simple, single motor pattern. Instead, successfully acquiring banana pieces depends on engaging a sequence of several consecutive steps. While the control animals occasionally pulled the door but immediately released it, that is, they only tried to open it in this way, some observers also found a way to keep the door open by using other body parts while reaching for the bananas. This fundamental difference between trial and error learning on the one hand and the fluent as well as successful execution of a compound action on the other represents the qualitative, rather than the quantitative, difference between the behaviour of an imitator and the behaviour of an inexperienced animal.

Because we found strong individual differences in the observer group it is worth examining the test performance of individuals in addition to that of groups. Furthermore, since the experimental design alone cannot provide a control for several non-imitative effects, such as emulation or observational conditioning, we added a microanalysis of the individual execution of the initial actions at the manipulandum.

Unfortunately, pursuing the latter approach inevitably leads to major theoretical problems. At present there is no commonly accepted classification scheme for all phenomena that have been reported in the past. While psychologists have created such a scheme from an 'animal learning theory' point of view (Galef 1988; Rescorla 1988; Heyes 1994), comparative cognitivists have used a more 'ethological' approach (Whiten & Ham 1992; Byrne 1994; Moore 1996; Whiten & Custance 1996). The recent debate between Heyes (1995) and Byrne & Tomasello (1995) has shown convincingly that both attempts cannot easily be mapped onto each other. What follows is an attempt to interpret our results using the most appropriate terms, irrespective of the systematics from which they stem.

An analysis of the performance of the observer subjects during the test phase suggests the occurrence of three main categories of imitation-like

Table II. Techniques of pulling and pushing of all animals during the first test session

	Technique in pulling (%)					Technique in pushing (%)				
	Handedness					Handedness				
Subject	Left	Right	Claws in lateral gap	Hook*	Fingers in horizontal gap	Left	Right	Claws in lateral gap	Head	Arms
Model										
JU	79	21	33	67	0	—	—	—	—	—
Observers										
CS	100	0	29	71	0	0	100	100	0	0
SU	92	8	35	65	0	25	75	0	50	50
GO	40	60	60	0	40	81	19	0	0	100
LA	20	80	60	40	0	58	42	0	6	94
SH	0	0	0	0	0	0	0	0	100	0
Controls										
HA	0	16	8	7	0	0	9	0	1	4
HE	1	10	8	2	1	12	28	0	3	36
IV	3	0	0	3	0	2	0	0	0	1
IR	0	1	0	1	0	1	0	0	2	0
AA	0	0	0	0	0	0	0	0	7	0
AL	90	10	80	20	0	0	100	0	68	32

The proportions of using the left or the right hand as well as the proportions of using one of three techniques of pulling and pushing are shown. The corresponding data of the model are included.

*Pulling the pendulum-door by clutching the hook with fingers or only with claws (see Fig. 2).

behaviour. (1) Subjects LA and SH seem not to have profited from the opportunity to observe a skilful conspecific, and instead solved the problem through trial-and-error learning. However, the acquisition speed of the solution and the initial efficiency suggest that even those subjects had gained some information from observing the model. The prime candidate for such a facilitation effect is stimulus or local enhancement in combination with skill learning. The possibility of observing a conspecific manipulating a pendulum-door immediately before getting banana pieces from inside the box may have directed their attention to this small part of the laboratory environment, whether it was the test apparatus (local enhancement) or the manipulandum (stimulus enhancement). Compared with naive animals, rapidly learning to act adequately at the wooden box may also be due to reduced exploration of the new object (only brief olfactory exploration).

(2) Subject GO differed from the above-mentioned animals by initially trying pulling, and from the subjects CS and SU by using a unique technique. It is the latter aspect that makes the behaviour of this subject, and also the acts of the two close copiers CS and SU, more interesting. Inserting the finger into cracks and chinks of trees is a common foraging technique of callitrichids. We therefore suggest that subject GO had taken advantage from observation by incorporating the goal of 'pulling the door' into her own senso-motoric schemata. If GO had really learned to understand a change in the state of the world produced by the manipulations of the model, then, following the description of emulation learning (Tomasello 1990), she may have used what she had learned in devising her own behavioural strategies. In the initial demonstration of this imitation-like effect, Tomasello et al. (1987) found young chimpanzees, *Pan troglodytes*, inventing their own technique of raking in out-of-reach food with sticks. Obviously, it is not necessary to suggest that the animal has acquired insight into the goals of a conspecific or its intentions ('goal emulation' after Whiten & Ham 1992), but that it learned from the demonstrator the 'affordances' (Gibson 1979) of the tool associated with the food (Tomasello 1996). For instance, GO may have recognized some causal relations between the compound stimulus of the pulled door with the model beneath it and the availability of food.

(3) Finally, we are confident we witnessed the strongest facilitating effects of social learning in the behaviour of the subjects CS and SU. Both the high number of repetitions of the model's demonstrated behaviour and the nearly exact copying of the form of this action is evidence for true (visual movement) imitation. Following Zentall (1996), we support our argument by applying three criteria for true imitation in the sense of Thorpe's definition: 'By true imitation is meant the copying of a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency' (Thorpe 1956, page 122).

First, we may ask whether the copied target behaviour is already part of the observing animal's repertoire. Unfortunately, this will remain an undecidable question until we agree on the level of investigation. Clearly, at the level of muscle twitches both individuals manipulated the pendulum-door within the constraints of genetically determined motor programmes. At the next hierarchical level, the analysis of the arm movements, it is plausible to suggest that pulling arises from basic motor programmes of the limbs, especially if one considers the inherent flexibility of arboreal species. However, at the level of the shape of the action, we find such a high similarity in form between model and observer that a fixed species-specific motor programme (in the sense of a fixed action-pattern) is unlikely. Indeed, all the monkeys used in our experiment have sooner or later shown pulling attempts. But neither was any subject as adept in performing this technique nor as efficient in using it than the subjects CS and SU. While others used a different arm or seized a different part of the pendulum-door or failed to keep the door open when pulled, these two observers executed every element of the pulling action in the correct sequence and with sufficient proficiency.

Estimating the proportion of novelty in imitated behaviour has been discussed at length in recent papers. Whiten & Custance (1996), for instance, emphasized that novel imitations probably cannot arise de novo but are instead derived from what is already in the repertoire. In our opinion, selecting a novel task involving (1) some improbable movements, (2) the comparison with non-observers that show significant deviations of the crucial action, and (3) a microanalysis of the behaviour performed at the first opportunity (including a special focus on the details of form

Table III. The MANOVAs of five linear models investigating the influences of four predictor variables on the number of explorations, the number of manipulations, the rate of pulling, the efficiency in pulling and the efficiency in pushing

	MANOVA		Previous experience		Individual differences		Session		Sex	
	$F_{4,50}$	*P*	*T*	*P*	*T*	*P*	*T*	*P*	*T*	*P*
No. explorations	13.909	<0.001	2.881	<0.01	− 0.337	NS	− 5.022	<0.001	0.038	NS
No. manipulations	2.138	NS	0.378	NS	0.605	NS	− 0.755	NS	− 1.580	NS
Pull rate	6.751	<0.001	1.873	<0.1	− 3.806	<0.001	− 1.832	<0.1	− 0.438	NS
Pull efficiency	16.267	<0.001	− 3.071	<0.01	− 0.901	NS	1.054	NS	− 0.901	NS
Push efficiency	11.177	<0.001	− 1.785	<0.1	− 1.083	NS	2.134	<0.05	1.424	NS

and sequence) should provide us with a sound basis for postulating true imitation in two of five observer subjects.

Taking Thorpe's definition strictly, we need not rely on the criterion of novelty. Owing to the difficulties mentioned above it is much more convenient to use the alternative criterion of improbability of an act. By estimating the a priori probability of the spontaneous replication of the model's pulling behaviour in any naive subject we found it highly improbable that such a combination of movement elements occurs by chance. As a consequence it strongly supports our suggestion that the two subjects CS and SU have learned about the instrumental solution of the presented task by observation.

The second criterion for true imitation refers to the distinction between immediate or delayed imitation, that is, whether motivational effects, produced by the mere presence of a demonstrator, are absent during the execution of the observed behaviour (Zentall 1996). In applying delayed conditions in our experiment, namely requiring the observer to hold in memory the behaviour it has observed, we could both control for social facilitation and prevent retardation of the acquisition of a new response caused by the presence of the demonstrator (Zajonc 1965; Huang et al. 1983).

Finally, to show that the test behaviour of the subjects CS and SU was not a socially facilitated reproduction of an already existing motor pattern, a control for enhancement effects is necessary (Zentall 1996). As was the case in subject GO, the mere fact that CS and SU have demonstrated, relative to the control group and relative to the subjects LA and SH, a significant bias towards the execution of the non-preferred manipulation technique during the initial phase of the test makes it very improbable that these two observers have merely had their attention drawn to the manipulandum. Stimulus enhancement and subsequent trial-and-error learning used to be a powerful explanation for many imitation-like phenomena that involve earlier approaching and tool manipulation in observers relative to non-observers. Even the famous cases used as examples of imitative social transmission, that is, milk-bottle opening by tits (Fisher & Hinde 1949) and sweet potato washing by Japanese macaques (Kawai 1965), can now be explained in terms of a combination of enhancement and autoshaping (Sherry & Galef 1984; Galef 1990; Moore 1992). However, these kinds of pre-imitative processes are insufficient to explain why the subjects CS and SU opened the pendulum-door in exactly the same manner as the demonstrator. The two-action method we used allows us to rule out simple stimulus enhancement; and the exact match of the pattern of spontaneous responding on the first opportunity is clear evidence for discarding autoshaping.

Instead, in contrast to the non-observers and the three observers discussed above, subjects CS and SU acquired their initial test behaviour through precise and faithful copying of the observed manipulative actions performed by the model. Even programme-level imitation is an unlikely explanation for these results (Byrne 1994); the comparison of the actions between the model and these two observers transcends similarity of the logical structure of pulling. Although no imitation will be exact in all its details, it is sufficient to involve replication in outline or the copying of several features of the response pattern (for a broader discussion of this issue see Whiten & Custance 1996 and Russon 1996). As mentioned above, our microanalysis of the two subjects' actions revealed a very high position on the dimension of copying fidelity (Whiten & Ham 1992; Byrne 1994). This is remarkable insofar as a recent study applying comparable methods using children and chimpanzees has revealed a considerably stronger tendency in the latter to use their own methods (Whiten et al. 1996). However, this significantly lower level of faithfully copying the model's acts may have resulted from a much more complex task (involving an apparatus consisting of three component parts with two manipulation techniques each) and a more restricted opportunity to watch a demonstrator performing the required technique (Whiten et al. 1996).

Finally, we may ask why the pulling behaviour acquired through precise and faithful copying was lost through relearning the pushing technique. Moore (1996) recognized that visual movement imitation can teach only the rudiments of solving a complex task involving new movements, while subsequent skill learning completes the individual solution. The necessity of supplementing both kinaesthetic and proprioceptive information as well as of experiencing reinforcement on its own actions is well documented in termite-'fishing' chimpanzees (Goodall 1971). Although there are at present only vague suggestions about when and why imitated behaviour declines or disappears (Tomasello 1996), there is some evidence that imitated behaviour, like other acquired behaviour, is not insulated from modification by susbequent trial-and-error learning (Galef et al. 1986; Heyes 1993; C. M. Heyes, E. Jaldon, E. Ray & G. R. Dawson, unpublished data). Similarly, our two subjects have gathered their own experiences in opening the banana box, some of them probably accidentally, and have subsequently refined their techniques. According to Tomasello (1996) we may use the term ‘mimicking’ instead of imitation in order to denote the fact that the reproduction of behaviour on the sensory–motor level does not require the observer to understand the intentions of the model. Imitation may then be reserved for cases where observation leads to the perception and understanding of how the behaviour is designed to bring about the goal or to acquire insight into the causal structure of a problem. Beyond the cognitive perspective, and from an ethological point of view, we are primarily interested in whether a monkey species such as the common marmoset is capable of perceiving or conceiving a correspondence between the behaviour of a skilful model and its own behaviour, which allows some kind of reproduction.

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