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Stimulus Enhancement and Spread of a Spontaneous Tool Use in a Colony of Long-tailed Macaques

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ABSTRACT. In a captive group of long-tailed macaques, tool-using behavior by a single competent individual had a significant effect on the synchronous manipulative behavior of naïve animals. Group members engaged in manipulations on the same object class more frequently during times when the model was working than when it was not. The form of their behavior, however, in no way resembled the technique used by the model. All three animals that later became successful tool users were among the few subjects that exhibited a significant increase in manipulations on the same object class while the model was working. Possible causal relationships between this stimulus enhancement and the transmission of the new behavior to other group members are analyzed and discussed.

Key Words: Non-human primates; *Macaca fascicularis*; Social learning; Stimulus enhancement; Tool use.

INTRODUCTION

The study of mimetic behavior in animals has been of central interest for more than a century, partly because of its importance in understanding transmission mechanisms in human cultures. Most scientific efforts have focused on non-human primates, which have been regarded as having a special aptitude for imitation (see PASSINGHAM, 1982 for a review). Observers of the Japanese macaques living on Koshima Islet and Takasakiyama reported three different inventions of food processing (potato washing, placer mining, and caramel eating) by a single subject, which seemed to have been transmitted to other group members (see NISHIDA, 1987 for a review). These cases have long been interpreted as cultural transmissions through imitation (e.g. PREMACK, 1984, p. 17; MCFARLAND, 1985, p. 514).

More recent work has questioned this interpretation (e.g. GALEF, 1990; WHITEN & HAM, 1992). For the Koshima phenomena, WHITEN and HAM (1992) have proposed the label "stimulus enhancement," defined as a change in the orientation of an observer's behavior toward stimuli associated with previous reinforcement of a demonstration behavior (BECK, 1976), whereas imitation is viewed as the acquisition of the capacity to execute a behavior using movement patterns that are topographically similar to the observed conspecific behavior (HEYES, 1993). Using these definitions, experimental studies of imitation on monkeys have produced mostly ambiguous results, with no case where claimed evidence of imitation could not have been interpreted more parsimoniously (see WHITEN & HAM, 1992 for a review). One reason for this debate might be purely semantical, however. There is no uniformly accepted taxonomy of social learning mechanisms at present (e.g. GALEF, 1988; WHITEN & HAM, 1992; HEYES, 1993). The observation that one animal's behavior can influence that of another has produced a rich and bewildering vocabulary of social learning phenomena, while at the same time providing little empirical basis for any meaningful classifications of the phenomena into distinct, biologically meaningful categories (GALEF, 1988).

A spontaneous invention of a new food retrieving technique by a single individual in our group of long-tailed macaques (*Macaca fascicularis*), followed by subsequent invention by or transmission of the technique to other animals, allowed us to observe an immediate effect of the model's behavior on other group members.

On August 27, 1991, the high ranking male *MD* was observed by CHARLES MENZEL spontaneously to use wooden sticks scattered about to rake in apples that had fallen from a tree outside the enclosure. In September 1991, *MD* became the alpha male of the colony. It soon appeared that naïve individuals were more likely to manipulate objects during times when *MD* was engaged in raking in fruits compared to times when he was not working. Using the taxonomy of WHITEN and HAM (1992), we assumed that stimulus enhancement could account for the observed phenomenon. To test this hypothesis, we controlled *MD*'s temporal and spatial access to fruits, i.e. we limited access to fruit outside the wire net to 30 min sessions, usually once a week. During these sessions, we presented one fruit at a time at a fixed distance from the wire and replaced it when it was consumed. *MD* was generally well motivated and performed as a reliable model. This allowed us to compare the manipulative behavior of other group members during times when fruit access was granted as opposed to control periods with no fruit access. We were primarily interested in the following three questions. First, is there a stimulus enhancement effect, and if so, what aspects of the behavior are transmitted from the model to naïve observers: the choice of object class and shape, the movement patterns used in raking and/or the orientation of the tool to the fruit? Second, what is the temporal course of the stimulus enhancement effect? Third, can stimulus enhancement predict which other animals will acquire the tool-using behavior in the future?

METHODS

SUBJECTS

Subjects were a colony of 35 – 37 long-tailed macaques *Macaca fascicularis* (12 – 13 males and 23 – 24 females) housed in a large indoor/outdoor enclosure of approximately 1,000 m^2. The colony has existed for more than ten years.

OBSERVATIONAL SCHEDULE

This study extended from April 1992 to September 1993. At the time of the study the apple tree adjacent to the enclosure had died and the only fruit now available outside the enclosure was provided by experimenters during observation sessions of 30 min.

Pieces of fruit (mostly apple) were positioned at a distance of usually 30 cm from the outer edge of the foundation wall of the enclosure during 'session periods.' This procedure guaranteed that the only way a monkey could get hold of the fruit was by using a tool of at least 20 cm in length. This tool had to be pushed through a 5-cm wide horizontal gap between the foundation wall (height 10 cm) and the enclosure fence (height 3 m). The enclosure itself provides a large variety of manipulanda with differential usefulness as tools, such as sticks and twigs, small boards, pieces of bark, and the rounded stones (2 to 20 cm in diameter) of a gravel surface.

As soon as a fruit was retrieved into the cage an observer positioned another fruit on the same place. If a monkey caused a displacement of the fruit and gave up its retrieving activities by leaving the working area, the fruit was repositioned to the original spot.

A video camera recorded the whole 30-min session period from a distance of approximately 1.5 m. Verbal comments on the identity and behavior of individuals in the work area were given by the observer ad lib.

DEFINITIONS

Session period: A continuous half-hour period consisting of 30 1-min intervals during which pieces of fruits were successively positioned outside the foundation wall.

Control period: A continuous half-hour period consisting of 30 1-min intervals during which no fruits were positioned. All but two control periods preceded the session period by about one hour.

Observation field: A part of the outdoor enclosure, adjacent to the working area, of about 200 m^2, containing many sticks, branches, ropes, stones, a climbing frame, and a pond.

Working area: An area in the observation field described by a semicircle with a diameter of 3.5 m. The secant of the semicircle is formed by the interior side of the foundation wall.

Model: An animal that was actively trying to rake in a piece of fruit with a tool.

Skilled animal: An animal that at least once had successfully retrieved a piece of fruit with a tool.

Naïve animal: An animal that had never successfully retrieved fruit with a tool.

Manipulation: Causing a locational change on an external object that was free of any fixed attachment to the substrate with one or both of the actor's hands.

Manipulation bout: A bout began when the actor grasped an object and ended when it released it.

Wooden object: Any ligneous plant matter at least 5 cm long.

Stone: Any solid (but not metallic) mineral matter with a diameter of at least 3 cm.

DATA COLLECTION

The following parameters were recorded for both session and control periods: (a) Number of naïve animals present in the observation field at the beginning of each of the 30 1-min intervals. All 30 values summed constitute the value 'total presence' in that period; (b) Number (and identity) of naïve animals manipulating mobile wooden objects in the observation field some time during the first 10 sec of each of the 30 1-min intervals. All 30 values summed constitute the 'wood manipulation score' in that period; and (c) A 'stone manipulation score' was calculated in the same way.

Manipulation of live plants was not recorded. We also recorded how long each individual was present in the working area during session periods, and how many bouts of manipulation it performed there.

DATA ANALYSIS

Positioning of fruits during session periods tended to attract more animals to the observation field than at other times and hence increased the chance of manipulations due to sheer number. Therefore the 'relative manipulation score' was calculated for all session and control periods, for wood and stone separately, as the 'manipulation score' divided by 'total presence.'

HYPOTHESES

Successful fruit retrieval is only possible if an animal selects for certain object features when choosing a tool. Length clearly is most critical, for animals must be able to cause physical contact with the fruit in order to rake in it. No stones were long enough and at the same time thin enough to reach the fruit. *MD* hardly ever tried to use stones to retrieve the fruit, but consistently picked sticks or lengthy pieces of bark to solve the task. Under the assumption that stimulus enhancement is only activated with an appropriate match of manipulanda, we expected animals to have a higher manipulation rate on wooden objects, i.e. an increased 'relative wood manipulation frequency,' and an unaffected manipulation rate on stones, i.e. an unaffected 'relative stone manipulation frequency' during session periods as compared to control periods.

RESULTS

TRANSMISSION OF OBJECT CLASS

Statistical analysis of stone manipulations revealed no significant difference between session and control periods for either year (Table 1). Wood manipulations, on the other hand, followed a time dependent pattern: All but one of the ten sessions in 1992 show a relative increase in manipulations in session times, which yielded a significant increase in 1992 (the large control value of July 2, 1992 was caused by three animals playing with sticks at the pool in the observation field during the control period). With the resumption of the data gathering process in April 1993, after a six-month winter break, this pattern was no longer apparent, and no significant increase for the group was observed any more (Table 1).

Thus, enhancement was limited in three ways: (1) It only elicited manipulations on objects of the same material as the model's tool; (2) it occurred only during periods when the model was actually working, not throughout the day; (3) it declined after the first five months. On the other hand (4) the enhancement was not limited to the area where the model was working, but was effective throughout the whole observation field.

TRANSMISSION OF OBJECT SHAPE

Due to the enriched housing conditions, monkeys had a large variety of shapes to choose from within the object class 'wooden things.' Experienced tool users show a tendency to

Table 1. Relative manipulation scores in all control-session pairs, in the first two years of the model's tool behavior.

Test date		Wood		Stone	
		Control	Session	Control	Session
1992	May 26	**0.010**	**0.035**	**0.000**	**0.015**
	June 2*	**0.005**	**0.017**	0.041	0.023
	June 15	**0.018**	**0.062**	0.018	0.006
	July 2	0.295	0.065	**0.049**	**0.107**
	July 9	**0.006**	**0.007**	0.023	0.000
	July 16	**0.078**	**0.120**	0.047	0.017
	August 5	**0.025**	**0.223**	0.012	0.000
	October 8	**0.022**	**0.055**	0.067	0.060
	October 13	**0.000**	**0.025**	0.086	0.050
	October 29	**0.006**	**0.008**	**0.000**	**0.008**
Wilcoxon (one-tailed)		$T = 10$, $p = 0.05$		$T = 17$, n.s.	
1993	April 21	0.118	0.030	0.069	0.022
	April 27	0.080	0.040	**0.023**	**0.028**
	April 28	0.112	0.031	0.000	0.000
	May 18	**0.000**	**0.028**	**0.000**	**0.039**
	May 19	0.021	0.008	**0.000**	**0.004**
	June 1	0.000	0.000	0.000	0.000
	June 8	**0.000**	**0.034**	0.000	0.000
	June 15	0.033	0.006	**0.000**	**0.006**
	June 22	**0.000**	**0.030**	0.000	0.000
	June 29	0.000	0.000	0.000	0.000
	July 6	0.000	0.000	0.000	0.000
	July 13	0.000	0.000	0.021	0.016
	July 21	0.000	0.000	**0.051**	**0.068**
	July 27	0.013	0.000	0.103	0.007
	August 4	**0.018**	**0.030**	**0.009**	**0.015**
	August 11	**0.000**	**0.006**	**0.015**	**0.030**
	August 19	**0.007**	**0.010**	0.007	0.000
	September 16	0.000	0.000	0.059	0.031
Wilcoxon (one-tailed)		$T = 30$, n.s.		$T = 40.5$, n.s.	

*Session period before control period. Numbers in bold indicate an increased manipulation activity in session relative to control periods.

select lengthy thin sticks as tools. Although we did not quantify the shape criteria of wooden objects chosen by naïve animals, we believe that naïve animals did not show any preference for tools of the appropriate shape. Besides sticks, naïve animals manipulated anything they encountered from twigs, to boards, and to pieces of bark.

TRANSMISSION OF MOVEMENT PATTERNS AND ORIENTATION

Efficient tool users direct the tool's longest axis towards the fruit ('orientation') and apply a semicircular sweeping motion to knock a piece of fruit to a point within their reach ('movement pattern'). The fruit is hit on the lateral or distal side from the animal's point of view, which usually results in moving the fruit closer to the tool user.

Neither 'movement pattern' nor 'orientation' were transmitted from the model to the manipulators in the observation field. Naïve animals were never seen to exhibit the sweeping type movements a skilled animal applies to the task. Instead, they typically sat at elevated places several meters from the model, continuously altered the position of their grip on the tool, sniffed or bit it, released it, and picked it up again, as they would in spontaneous manipulation. Object movement was chaotic, non-oriented and never aimed at a target object. The manipulators did not face or noticeably observe the model or the fruit. Their attention seemed entirely on their own object.

INDIVIDUALS THAT ACQUIRED THE TECHNIQUE AFTER THE MODEL

Approximately one year after the first animal, *MD*, used a tool to retrieve fruit, a second adult male, *UK*, had his first success in retrieving a fruit with a stick. He was followed by a juvenile male, *TB*, nine months later, and finally by the adult male *MS*, another ten months later (Table 2).

Table 2. Data on "skilled male animals" (November 1993).

Animal	Birth	Rank	First success	Kin relationship to *MD*	Success rate
Madu (MD)	1982	High	August 27, 1991	—	High
Ukui (UK)	1981	High	August 4, 1992	Close: same matriline*	Low
Tubau (TB)	1990	Low	May 18, 1993	Far: other matriline*	High
Masuk (MS)	1986	Middle	June 8, 1993	Close: same mother	Low

*Of the total of the four.

Table 3. Wood manipulation scores of all subjects that showed more wood manipulations in session periods compared to control periods (11 out of 35 animals).

	Frequency of wood manipulations in session and control periods (individuals)																					
	Male										Female											
	TB		*MS*		*SB*		*TF*		*UK*		*JE*		*TD*		*RT*		*SA*		*DA*		*MR*	
Test date	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S
1992																						
Apr. 07″	–	4	–	8	–	3	–	16	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apr. 28	–	3	–	–	–	–	1	–	–	2	–	–	4	1	–	–	–	–	–	–	–	–
May 01	–	6	–	2	–	3	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–
May 05	–	–	–	3	–	–	–	1	–	1	–	–	–	1	–	–	–	1	–	2	–	2
May 12	–	3	–	3	–	5	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	1
May 26	–	3	–	–	–	1	–	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–
June 02″	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
June 15	–	1	–	2	–	1	–	–	2	2	–	–	–	3	–	–	–	1	–	–	–	–
June 21	–	2	–	–	4	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
July 02	–	2	–	–	–	2	–	4	–	–	–	2	–	1	–	–	–	–	–	–	–	–
July 09	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
July 16	–	–	–	–	–	8	6	–	–	–	–	1	–	5	–	2	–	1	–	1	–	1
Aug. 05	–	7	–	7	–	4	–	15	–	–*	–	7	–	3	–	–	–	1	1	–	–	–
Oct. 08	5	8	–	–	–	2	–	–	–	–*	–	–	–	–	–	1	–	2	–	–	–	–
Oct. 13	–	3	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oct. 29	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–

(continued)

Table 3. (continued)

	Frequency of wood manipulations in session and control periods (individuals)																					
	Male										Female											
	TB		*MS*		*SB*		*TF*		*UK*		*JE*		*TD*		*RT*		*SA*		*DA*		*MR*	
Test date	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S
1993																						
Apr. 21	2	4	–	1	–	2	–	–	–	5	–	–	–	–	–	–	–	–	–	–	1	–
Apr. 27	1	5	–	–	–	1	–	–	–	12	–	–	–	–	–	–	2	–	–	–	4	1
Apr. 28	10	5	–	1	1	1	4	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
May 18	–	4*	–	4	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
May 19	6	2*	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
June 01	–	6*	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–
June 08	–	5*	–	2*	–	–	–	7	–	–*	–	–	–	–	–	–	–	–	–	–	–	–
June 15	–	1	–	6	2	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
June 22	5	11	–	7	–	3	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
June 29	–	4*	–	2*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
July 06	–	11*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
July 13	6	7*	–	7	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
July 21	10	8*	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
July 27	11	15*	2	2	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aug. 04	13	10*	3	1	–	2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	1
Aug. 11	–	8*	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aug. 19	7	7*	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Sept. 16	3	4	16	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
	$z=3.39$		$T=22$		$T=19$		$T=19$		$T=19$		$T=3$		$T=4$		–		$T=5.5$		$T=2$		$T=9.5$	
p	<0.005		<0.005		<0.005		n.s.		<0.005		<0.05		n.s.		n.s.		n.s.		n.s.		n.s	

Entries indicate the number of 1-min intervals (max 30) in which an animal manipulated at least one wooden object during the first 10 sec of that interval. Thus, animals can successfully retrieve fruit and still have no entries at all if they consistently manipulate out of the 10 sec period. This happened repeatedly with *UK*, who manipulated his tools discontinuously and at a relatively low rate, but still managed to achieve some successes. Wilcoxon (one-tailed) for increase in wood manipulations of session compared to control periods. *TB*, *MS*, & *UK*: Skilled animals; C: control period; S: session period; –: no wood manipulations observed; ″ session period before control period; * success.

So far we have treated the stimulus enhancement effect as a group phenomenon. In an attempt to assess the influence of stimulus enhancement on the transmission of the new technique to other animals we examined how each animal was affected by stimulus enhancement (Table 3).

Not all animals were equally affected by stimulus enhancement: only 11 of 35 animals showed increased wood manipulations during the session periods for both years. This increase was individually significant for only five animals (Table 3). Four of these five individuals were males. Three of the four individuals acquired the raking technique (Table 4).

Table 4. Relationship between developing the skill and prior stimulus enhancement (until November 1993).

	No. of males		No. of females		
Stimulus enhancement	Skilled	Unskilled	Skilled	Unskilled	Total
Significant	3	1	0	1	5
Not significant	0	5	0	22	27
Total	3	6	0	23	32*

*Without *MD* and two dependent infants.

STIMULUS ENHANCEMENT AND THE SPREAD OF TOOL USING BEHAVIOR IN THE GROUP

Some social learning mechanisms can be excluded a priori, such as imitation since *MD*'s behavior pattern was not reproduced. Social facilitation can also be excluded because not only the time of the manipulations but also the object class were taken over by observers. In contrast, stimulus enhancement cannot be excluded as a learning mechanism, for the null hypothesis that skilled and naïve animals are equally likely to be affected by stimulus enhancement can be rejected (Table 4, Fisher-test, $p < 0.01$).

All three individuals that did learn the new behavior pattern (*UK*, *MS*, and *TB*) showed significantly more wood manipulations during session periods relative to control periods, while two more individuals (*SB* and *JE*) showed significantly more manipulations but failed to learn the new behavior until the end of the 1993 season (Table 3). Thus, stimulus enhancement alone does not seem to suffice as a mechanism that allowed animals to acquire the new behavior. None of the 35 animals showed a significant increase in stone manipulations during session periods. Hence, it was not an inability to discriminate between the two object classes that accounted for the failure to acquire the new behavior in these two animals.

At the same time, we cannot conclude from these data that stimulus enhancement is a necessary prerequisite to becoming a skilled animal, because *MD*, the inventor of the technique, most likely developed his skill by means of individual learning, i.e. without stimulus enhancement. On the other hand, we cannot exclude that, prior to his first success, *MD* was enhanced on manipulating wooden objects by some other factor and then transferred this tendency to the fruit retrieving problem.

If stimulus enhancement is a cause for the acquisition of the new technique, we expect that enhanced and later successful animals should exhibit a higher proportion of wood to non-wood manipulations than other animals at the working area when a fruit is present (note that now we only compare manipulations at the working area, not in the whole observation field as before). In contrast, if 'local enhancement' (THORPE, 1963) was the main social learning mechanism accounting for the spread of the skill, we would expect the

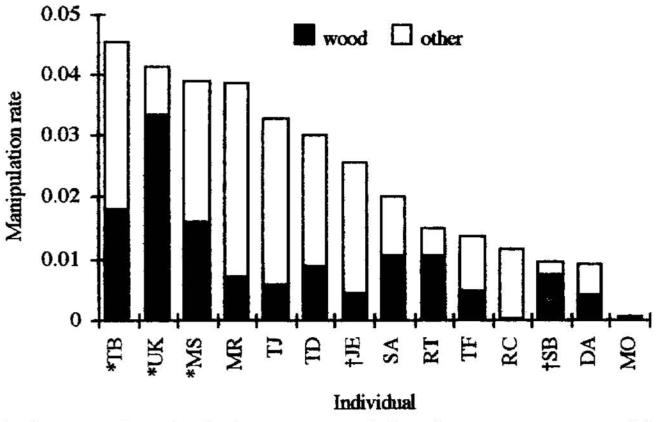

Fig. 1. Manipulation rate (manipulations corrected for time present at working area) for all individuals with total presence at working area of ≥120 sec. *Skilled and enhanced; †: enhanced only; MO: mean of 19 others with <120 sec total presence each (data until July 16, 1992).

general manipulation rate on any object class at the working area to be higher for the three skilled animals compared to other animals. Figure 1 presents data that favor both explanations. The three skilled animals exhibit the highest manipulation rates but also are among those with the highest proportions of wood to non-wood manipulations.

The three future performers of the skill also differed from others in that their manipulations in the observation field were continued into the second year; *TB*, the most successful of the three, began to manipulate wood even during control periods (Table 3). He was observed using stalks to retrieve dandelion flowers through the wire. In 1994 he began to poke sticks into holes of a fallen tree with no apparent benefit.

Perhaps, then, these males were simply more motivated to manipulate wood, and this motivation independently induced both their learning and their responsiveness to the stimulus enhancement. We tested this hypothesis by comparing the wood manipulation tendency of the future performers (*TB*, *MS*, and *UK*) and of naïve animals in the *control* periods in the pre-successful tests (i.e. until July 16, 1992; data after the first success were not used because success could enhance the manipulation tendency of an animal). We found no greater wood manipulation tendency in future performers of the skill than in naïve animals (Table 3). Thus, manipulatory tendency alone did not lead to the acquisition of the technique. Stimulus enhancement remains a possible causal agent.

OTHER CAUSAL FACTORS

Additional causal factors are possible. First, during the time when only the model, *MD*, was retrieving fruit, the future performers were in the working area more often than others and thus could observe the model at close range. Since they manipulated wooden objects more often (Fig. 1), they had more opportunities to orient their manipulations toward the fruit. Second, the social relationship of the new performers with the model could have contributed to their success. Like the model, *MD*, four of the five animals that showed a significant increase in wood manipulations and all that became skilled animals were males (Table 3); the null hypothesis that the stimulus enhancement effect is independent of gender can be rejected (Table 4, Fisher-test, $p < 0.02$). Furthermore, the inventor of the tool technique soon became the alpha male. The attention that focuses on the dominant individual of one's own gender (CHANCE, 1961) could therefore be responsible for the intensity of stimulus enhancement and the subsequent spread of the tool-using behavior.

DISCUSSION

STIMULUS ENHANCEMENT AND FUTURE TOOL-USING BEHAVIOR

Since increased manipulations were only recorded at times when we caused tool-using behavior by *MD* by presenting fruits, and since the manipulations were performed on the same object class *MD* was using as a tool, we concluded that *MD*'s activity was the cause for these increased manipulations. However, we cannot reject a rather weak but alternative hypothesis that the mere presence of a piece of fruit during session times was causally responsible for the observed phenomenon. The necessary control, preventing *MD* from raking in fruits, was not practical.

Since the 'enhanced' individuals manipulated only objects of the same class but did not orient their behavior and did not show the same movement pattern as the model, we believe that stimulus enhancement as defined by BECK (1976) is the most appropriate term for describing the phenomenon.

Increased manipulations were observed in the whole observation field. Thus, continuous observation of the model at short distances does not seem necessary for an animal to become enhanced. It may, however, be necessary for acquiring the complete technique.

Our data show a relationship between stimulus enhancement and later acquisition of the tool technique. Whether the two factors are causally related is not clear, however. Other hypotheses are possible. Nonetheless, the data do contradict one possible interpretation: That individuals with a high manipulative tendency (1) could be enhanced more easily than others; and (2) could learn a new technique earlier simply because of that manipulative tendency. In 1992, when the enhancement effect was present, the three future performers did not show a higher manipulation score during control periods than eight animals that did not subsequently learn the technique (Table 3).

Once an animal is enhanced in its unspecified manipulation of wooden objects, it has to take several additional steps before successful tool use is possible. It has to (1) push the manipulandum through the gap between foundation wall and fence; (2) reliably bring it into physical contact with the fruit; and (3) carry out a sweeping or raking movement. *UK* and *MS* had not reached step (2) until the end of the 1993 season. Stimulus enhancement merely caused a change in the distribution of attention in conspecifics towards the environment. This may have promoted learning opportunities toward the behavior of the model. In the present study its promoting function has been slight.

Taken together, the data suggest that stimulus enhancement and greater attention to the model contribute to the spread of successful tool use in a synergistic way, and therefore that both individual and social learning are involved. Stimulus enhancement may lead to an increased probability of developing the new technique by (1) increasing and directing the manipulations of other animals to the relevant object class. In combination with 'local enhancement' (THORPE, 1963) and an attraction to the model it could result in (2) more stick manipulations in the working area. These two social learning mechanisms may then increase the chance of touching or moving a fruit with a tool and provide a basis for subsequent individual learning: Fruit movements might then (3) raise the general motivation of an animal and shape its technique by operant conditioning. In addition, if a monkey manipulates a stick outside the cage and near the fruit, it is prevented from executing certain behaviors, such as biting the stick. This might help to (4) constrain its manipulations into the right channel and contribute to the acquisition of successful performance.

STIMULUS ENHANCEMENT AND FUTURE SUCCESS

Our data suggest a relationship between the two phenomena. *TB*, who was enhanced consistently and most strongly, soon reached a very high success rate, whereas *MS* and *UK* showed less enhancement and a low success rate (Tables 2 & 3). Thus, a relationship between stimulus enhancement and future proficiency in the retrieval task seems possible. Clearly, stimulus enhancement cannot be both a necessary and sufficient prerequisite to become a skilled animal, for the inventor *MD* most likely did not benefit from it, and two animals (*SB* and *JE*) were significantly enhanced but failed to acquire the new behavior (Table 3).

CONDITIONS FOR THE OCCURRENCE OF TRANSMISSION

The major flaw of this and other studies certainly concerns the fact that it does not go beyond the descriptive treatment of social interaction effects on behavior. As GALEF (1988) points out, there is still a pressing need for investigations that analyze the conditions under which social learning occurs. In our study, why did only five animals show enhanced wood manipulations and why did only three of these (all of them males) proceed to use their manipulanda and became successful tool users after more than two years of presence of a model?

SUMITA et al. (1985) identified a possible factor that differentiates successful from unsuccessful subjects in an acquisition task of stone-tool use to crack nuts in captive chimpanzees. They found that successful subjects were more likely than unsuccessful subjects to observe demonstrations. Unsuccessful subjects, in contrast, seemed to be distracted by too great a desire for the nuts and their 'willingness' to observe the model seemed to depend on the model's identity. FRAGASZY and VISALBERGHI (1989) studied the behaviors related to acquisition of tool use in tufted capuchins and found that the primary predictor of success was the level of interest in the task. Observing others at the apparatus did not facilitate exploratory behaviors and tool contact in naïve animals. In contrast, animals performed exploratory behaviors more often when they were at the apparatus alone than when with another individual. The authors conclude that capuchins do not learn about instrumental relations by observation and that imitation does not play a role. For the Koshima macaques ITANI and NISHIMURA (1973) have proposed three channels through which new adaptive behavior can spread through a monkey troop: (1) via playmates, (2) via matrilines, and (3) via paternal care. These channels fail to explain the pattern of spread in our group (Table 2). However, as has been noted by the authors, such channels also affect proximity and contact between animals.

Differential access to the working area can hardly explain the propagation pattern in our study. Quite often, the site was unattended for longer periods because skilled animals were satiated and had lost interest in the positioned fruits. Subordinate animals now could and often did enter the working area. Thus, subordinate naïve animals had ample opportunities to manipulate tools at the working area without direct presence of high ranking animals. Nevertheless we cannot exclude that other social factors, such as maintaining a high level of social vigilance, kept many animals from spending much time at the working area and exploring the relevant relationships between tools, fruits, and their own behavior (see also VISALBERGHI & FRAGASZY, 1990).

One might object that the fruits presented were not attractive to some animals so that their level of motivation was too low to learn the task. In fact, however, the fruit was generally and highly preferred, and we had the impression that differences in the interest for the fruits was not a relevant predictor. After the alpha male *MD* had left, the site was often strewn with fruit remains, such as banana peel, which then were picked up and eaten by naïve animals who came running up quickly. Perhaps it was this frequent possibility of exploitation that kept some animals from learning the task. The only propagation pattern that does seem to be unusual is gender. Out of 33 animals that were physically capable of using sticks as tools, only 10 were males. Four of them learned the task whereas none of the 22 females appeared to have learned anything. Since the inventor was a high (and soon the highest) ranking male, the number of potential close observers may have been drastically diminished for social reasons. VISALBERGHI and FRAGASZY (1990) suggest that the transfer of novel motor skills is most effective in dyads where the learner does not pose any threat to the model, allowing the learner to participate intimately in the model's actions, as it will often be the case for mother-infant pairs. In our study, it was the dominant male *MD*, who invented the skill. Interestingly, the young male *TB*, who acquired the skill most rapidly and to a very high proficiency, regularly enjoyed *MD*'s protection in social conflicts and, as an infant, was often carried around by *MD*.

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