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Hand Preference and Tool Use in Wild Chimpanzees

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ABSTRACT. The hand preference of chimpanzees in their natural habitat was studied at Bossou, Republic of Guinea, West Africa. The quantitative difference in left/right hand use was small in food picking and carrying. In contrast, the chimpanzees employed either the right or left hand in nut-cracking behavior using a pair of stones. All adults and many adolescents and juveniles utilized one hand exclusively for holding a hammer stone. Left hand preference was more prevalent among adults. However, when adolescents and juveniles were included, there was no significant bias in the ratio of left/right handers. Nut-cracking behavior requires long-term learning of the fine manipulation of stones and nuts by both hands. Each hand has a separate role, and the hands work together in nut cracking. The differential and complementary use of both hands may be a prime factor promoting exclusive hand preference in chimpanzees comparable to that of humans.

Key Words: Chimpanzee; Hand preference; Laterality; Tool use; Stone tool; Nut cracking; Food picking; Bossou (Guinea).

INTRODUCTION

Studies on handedness in nonhuman primates have increased dramatically in recent years (FAGOT & VAUCLAIR, 1988a, b; KUBOTA, 1990; MASATAKA, 1989; MERCHANT & MCGREW, 1991; STAFFORD et al., 1990; WARD et al., 1990; WARD & HOPKINS, 1991). Some reports have examined hand preference in chimpanzees (BARD et al., 1990; BRESARD & BRESSON, 1983; FINCH, 1941; TONOOKA & MATSUZAWA, 1993). There is also new evidence of left hand preference in reaching for food among lemurs at the population level. MACNEILAGE et al. (1987) proposed a hypothesis for the evolution of primate handedness; namely, that in primate evolution, the left hand is specialized for visuo-spatial reaching while the right hand is for fine manipulation.

Although the above studies do contain important information, there has been a lack of information in two respects. First, investigations have been carried out mostly under artificial conditions in captivity rather than in the animals' natural habitats. Second, most previous studies measured hand preference in a single task such as reaching for food and found only a weak hand preference in contrast to the strong right-hand bias seen in humans. Two questions thus remain unanswered. First, does a hand preference exist within the natural environment in nonhuman primates, especially chimpanzees, the closest relative of humans? Second, is there any exclusive hand preference in nonhuman primates as in humans?

Answers to these questions should provide important information concerning the emergence and evolutionary process of hand preference in humans. Up to now, the characteristics of human hand use are known to be the exclusive lateralized hand preference at the individual level and the right-hand bias at the population level. A right-handed person prefers to employ the right hand exclusively to throw a ball, to manipulate a pair of chop-

sticks, or to hold a pen. The number of right handers exceeds that of left handers in any human population. Does any corresponding phenomenon exist in chimpanzees? Is such handedness a totally unique characteristic of humans?

We studied the behavior of a habituated but non-provisioned group of wild chimpanzees to seek evidence of handedness in their daily behavior within the natural habitat. We examined two different types of behavior: picking food and holding a hammer for nut cracking. Some parts of the present study have been reported previously (FUSHIMI et al., 1991; MATSUZAWA, 1991a; SUGIYAMA, 1991).

MATERIALS AND METHODS

The subjects were the wild chimpanzees (*Pan troglodytes verus*) living in a small group at Bossou, Republic of Guinea, West Africa. Their behavior and ecology have been investigated since 1976 by SUGIYAMA and his colleagues without artificial feeding. The present study is based on data collected during the following three study periods: (1) from October 1989 to February 1990; (2) from January to April 1991; and (3) from October 1991 to February 1992. The behavior, ecology, and social structure of the chimpanzees at Bossou have been described in detail by SUGIYAMA (1981, 1984, 1988, 1989a, b) and SUGIYAMA and KOMAN (1979a, 1987).

The Bossou group had 18 chimpanzees (excluding 0- to 1-year-old infants) during the first study period, and the number decreased to 17 at the end of the study. All the chimpanzees have been recognized individually since 1976. The focal animals for the investigation of hand preference were all older than 2 yrs, and their ages ranged from 2 to 43 (estimated) yrs. They lived mainly in primary and secondary forests, sometimes raiding cultivated fields.

The following two behavior patterns were chosen for the assessment of hand preference in the wild chimpanzees.

Food picking: The first measure was food-picking behavior, i.e. picking a food (fruit, young leaf, or some other material) from a branch and taking it into the mouth (Fig. 1). When

Fig. 1. A young female chimpanzee, *Yu*, picking a small fruit from a branch with her left hand and supporting her body with her right hand.

a chimpanzee picked a food, he/she usually employed one hand while supporting him/herself by the other hand to sit, to stand, or to hang from a branch. Until the chimpanzee left a particular feeding site, the same hand was usually employed repeatedly to pick and move food. A 'feeding bout' was defined as repeated food picking and moving to the mouth at a feeding site until the chimpanzee left the site or changed his/her picking and moving hand. During the first study period in 1989–90, only the number of bouts was counted. During the second study period, in January to April 1991, both the number of feeding bouts and the number of food pickings were recorded.

Hammer holding for nut cracking: The second measure of handedness was hard-nut-cracking behavior using a hammer and an anvil (Fig. 2). The chimpanzees of Bossou cracked oil-palm nuts (*Elaeis guineensis*) with a pair of natural stones (SUGIYAMA & KOMAN, 1979b; SUGIYAMA, 1981). To facilitate detailed analysis of the nut-cracking behavior, we set up an outdoor laboratory in which stones and nuts were provided (SAKURA & MATSUZAWA, 1991). All episodes of nut-cracking behavior were video-recorded in the experimental set-up within the natural habitat (FUSHIMI et al., 1991; MATSUZAWA, 1991a, b). The animals placed a nut on a stone anvil with, in many cases, the second and third fingers of one hand, and then cracked it holding a hammer stone with the other hand. In the natural habitat, direct observations of nut cracking were difficult for two reasons: the chimpanzees were timid under palm trees close to the human village, and the dense bush under the palm trees interfered with the observations.

The chimpanzee usually hit the nut repeatedly until it opened. Occasionally, he/she stopped or went away before cracking was achieved when other chimpanzees began to travel or there was some kind of disruption. Young chimpanzees often stopped hitting because of difficulty with cracking. If less-skillful hitting caused the nut to spring from the anvil, the chimpanzee picked it up and placed it again on the anvil using the same hand, while the other hand continued to hold the hammer. When cracking was completed, the chimpanzee took the kernel from the broken shell to eat, swept the surface of the anvil with the back of his/her hand that was not used for holding the hammer, and picked up another nut to be placed on the anvil. He/she then began hitting again. Further details of the nut-

Fig. 2. An adolescent male chimpanzee, *FF* (left), cracking a nut on an anvil stone holding a hammer stone in his right hand. A juvenile chimpanzee (right) is observing him.

Table 1. Frequency of hammer use for nut cracking.

				January – February 1990						January 1991 – February 1992					
				Bouts			Hits			Bouts			Hits		
Name	Sex	Age	Mother	R	L	Total	R	L	Total	R	L	Total	R	L	Total
Ka	F	43	?	58	0	58	167	0	167	1	0	1	1	0	1
Nn	F	40	?	0	0	0	0	0	0	0	0	0	0	0	0
TA	M	38	?	0	69	69	0	156	156	0	17	17	0	42	42
Fn	F	36	?	0	45	45	0	105	105	0	+	+	0	+	+
Jr	F	32	?	0	285	285	0	939	939	0	+	+	0	+	+
Vl	F	30	?	11	0	11	36	0	36	+	0	+	+	0	+
Yo	F	28	?	0	60	60	0	197	197	0	144	144	0	390	390
Pm	F	24	?	0	0	0	0	0	0	0	0	0	0	0	0
Ki	F	14	*Ka*	70	0	70	216	0	216	–	–	–	–	–	–
FF	M	10	*Fn*	37	0	37	95	0	95	+	0	+	+	0	+
PR	M	10	*Pm*	12	2	14	66	17	83	2	0	2	4	0	4
Vb	F	8	*Vl*	0	+	+	0	+	+	–	–	–	–	–	–
Ja	F	7	*Jr*	51	0	51	149	0	149	+	0	+	+	0	+
Yu	F	6	*Yo*	0	0	0	0	0	0	0	0	0	0	0	0
NA	M	5	*Nn*	+	0	+	+	0	+	14	1	15	34	3	37
Kk	F	3	*Ki*	33.5	22.5	56	107	74	181	–	–	–	–	–	–
Vl	M	3	*Vl*	0	0	0	0	0	0	0	9	9	0	58	58
Pl	F	3	*Pm*	0	0	0	0	0	0	+	0	+	+	0	+
Jk	F	2	*Jr*	0	0	0	0	0	0	0	0	0	0	0	0

Age indicates the age in years in 1990. Ages of more than 14 were estimated in 1976 when long-term studies were started. R represents right-hand use and L represents left-hand use in hammer holding for nut cracking. +: Nut cracking was observed by FUSHIMI et al. (1991) and MATSUZAWA (1991, unpub. data) but frequency data were not given; –: data were not available because the individual disappeared from the group during this study period.

cracking behavior and the development of the technique will be reported separately by FUSHIMI et al. (in prep.).

A 'nut-cracking bout' was defined as a series of hits from picking up a nut until completion of cracking or until a pause of more than 30 sec had elapsed (including leaving the site). Such pauses were mostly seen in juveniles and infants. The number of nut-cracking bouts and the number of blows made by each chimpanzee were counted. The hand used for holding the hammer was also recorded for each chimpanzee (Table 1).

The nut-cracking performances were recorded using a Sony Beta-Cam and a Sony 8-mm Handycam. In total, we obtained video recordings of nut-cracking behavior lasting for about 400 min in the first study period, 1261 min in the second study period, and 2736 min in the third study period. To count the frequencies and bouts of nut cracking, the present study sampled video records lasting for 400 min from the first period, 180 min from the second period, and 20 min from the third period. At least two of the authors analyzed the video tapes to identify each individual involved and to confirm the hand preference.

RESULTS

Food picking: For picking food from a branch and moving it into the mouth, all chimpanzees used either the right or left hand during a feeding bout (Fig. 3a). Left/right bias in hand preference as measured from the number of feeding bouts was not significant, except in one chimpanzee (*PR*). The data for the first two study periods were consistent with each other ($s=0.324$, Kendall's rank correlation).

As regards the number of food pickings rather than feeding bouts, there was an inclina-

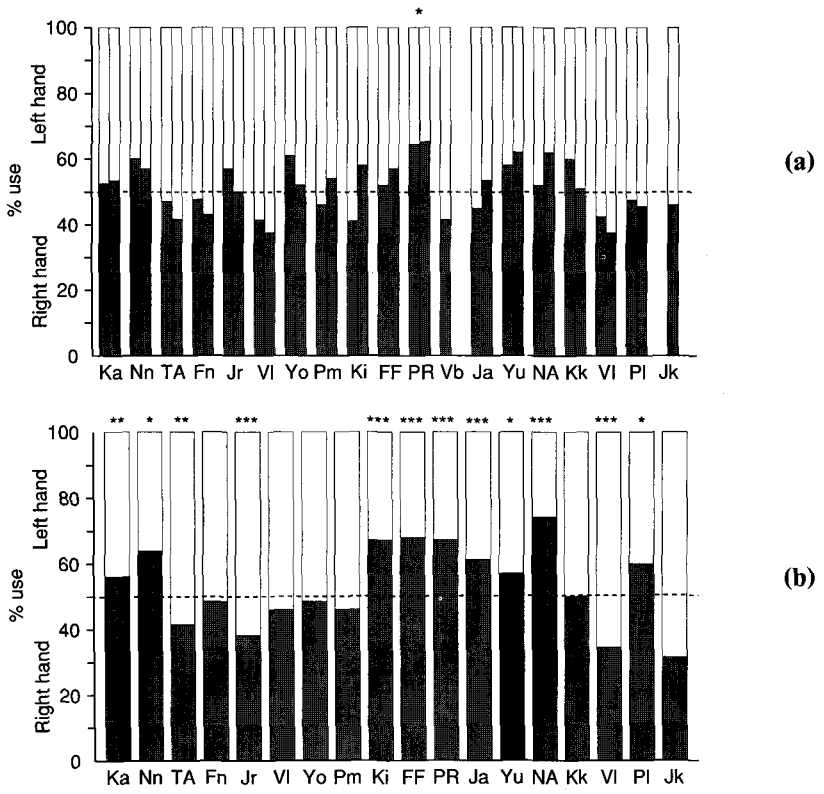

Fig. 3. Handedness in food picking (and transporting) during feeding in a tree. (a) Number of feeding bouts. Left columns: 1989–90; right columns: 1991. Left (white) or right (shaded) hand use. $*p<0.05$. (b) Number of food pickings (1991). $**p<0.01$; $***p<0.001$. The difference was evaluated by the binominal test. In the first study period of 1989–90, *Jk* was 2 yrs old and the sample number for her was too small for analysis. *Vb* disappeared before the beginning of the 1991 study period. In February 1991, *PR* had a badly injured left hand and could not use it properly. The left-hand fingers of *Nn* were malformed and she was unable to use them for fine work.

tion to use a particular hand. Some chimpanzees displayed a significant difference in their hand use (Fig. 3b). Nine were right-hand users, three left-hand users, and six did not show any significant hand preference (binominal test). This tendency for handedness in each chimpanzee was significantly correlated with that measured from the number of picking bouts in the second study period ($p<0.01$, $s=0.634$, Kendall's rank correlation).

Overall, the most important point was that the chimpanzees' food-picking behavior showed only a weak hand preference for the individual and no significant bias at the population level. The tendency for a preferred hand had no relation to age and sex.

Hammer holding for nut cracking: The hand preference in hammer holding displayed a clear exclusivity. All adults more than 12 yrs old (from *Ka* to *Ki* in Fig. 4) always employed a particular hand exclusively, although there was no left/right bias at the population level. This result was also confirmed by an episode monitored through direct observation: *SK*, an immigrant male living in the Bossou group during 1982–83, was seen to

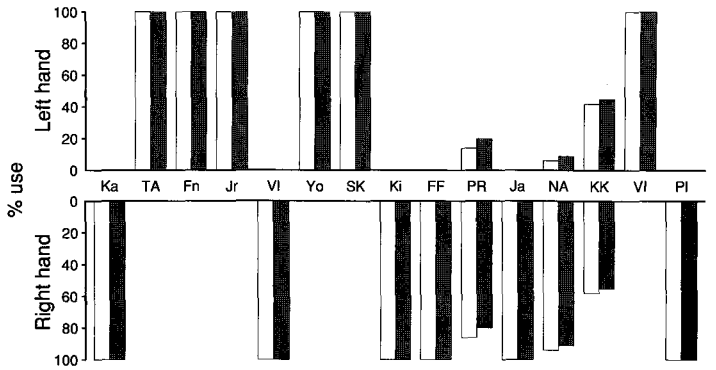

Fig. 4. Handedness in hammer holding for nut cracking. Number of bouts (white) and number of blows (shaded). *Nn*, *Pm*, *Yu*, and *Jk* did not perform nut cracking. *Vb* disappeared before the 1990–91 study period.

perform nut cracking in five bouts and nine hits exclusively with his left hand (SUGIYAMA, 1989a).

Immature chimpanzees (from *FF* to *Pl* in Fig. 4) also showed a strong hand preference for their hammering hand with a few exceptions. One adolescent male (*PR*), a juvenile male (*NA*) and an infant female (*Kk*) did use either hand. The latter two, *NA* and *Kk*, were observed to change the hand holding the hammer during a single bout.

Among the adult chimpanzees, five used the left hand exclusively to hold the hammer, and three used only the right hand. However, including adolescents (8–11 yrs), juveniles (4–7 yrs), and infants (< 3 yrs), the number of right-hand users became eight and left-hand users six (considering the hand preference of *PR* and *NA* as right). This implies that there is a strong and almost exclusive hand preference at the individual level but no left/right bias at the population level.

The heredity of hand preference was also analyzed. Table 2 shows a comparison within mother-offspring (five) or brother-sister (one) pairs. Among the six pairs, three (*Ka-Ki*, *Ki-Kk*, and *PR-Pl*) employed the same hand while the others (*Fn-FF*, *Jr-Ja*, and *Vl-VI*) employed the opposite hand. Based on these data, there seems to be no heredity of hand preference.

Acquisition of the nut-cracking skill is also independent of the skill of the mother. Two full-grown adult females, *Nn* and *Pm*, ate broken pieces of kernel produced by other mem-

Table 2. Relation of hand preference between food picking and hammer holding and between mother and offspring.

Head of kin	*TA*	*SK*	*Ka*			*Nn*		*Fn*		*Jr*		*Vl*			*Yo*		*Pm*		
Child				*Ki*			*NA*		*FF*		*Ja*	*Jk*		*Vb*	*VI*		*Yu*		*PR*	*Pl*
Grandchild					*Kk*															
Food-picking	L	-	(R)	R	RL	R	R	RL	R	L	R	RL	RL	-	L	RL	(R)	RL	R	(R)
Hammer-holding	L	L	R	R	(R)	-	R	L	R	L	R	-	R	-	L	L	-	-	R	R

Children are connected with their mother (head of kin) by horizontal and vertical lines. L=Left-hand users; R=right-hand users; RL: ns; ( ): $p<0.05$; others: $p<0.01$; −: no observation record.

bers but did not attempt to use stones even when others were cracking nuts with stones only a half meter away. These two females had not learned to crack nuts with a set of hammer and anvil stones. However, their offspring, *NA*, *PR*, and *Pl*, had no difficulty in cracking oil-palm nuts with stones.

The skill is not genetically transmitted to the next generation. *Yu*, who was 7 yrs old in 1991, failed to crack nuts even though her mother cracked nuts with stones. She placed a nut on an anvil and tried to crack it using her own right knuckle or right heel, but never used a stone-hammer. She was seen to snatch the kernel from a nut cracked by her mother like an infant or to forage the broken pieces of the kernels. Her behavior was thus not different from that of a young infant.

Correlation between food picking and hammer holding: Table 2 also shows the correlation in hand use for food picking and hammer holding during nut cracking. Chimpanzees who used the left (or right) hand for food picking also used the left (or right) hand in hammer holding. There were no chimpanzees who revealed a left-right discrepancy between food picking and hammer holding.

DISCUSSION

The wild chimpanzees of Bossou clearly revealed an almost perfect hand preference at the individual level when they held a hammer for nut cracking. However, such a strong hand preference was not observed in food picking, the common manipulative behavior reported throughout nonhuman primates in their natural habitat. The chimpanzees used the right and left hand almost equally in terms of the number of feeding bouts, although some displayed a weak hand preference at the individual level in terms of the number of food pickings.

The tendencies for hand preference in hammer holding and food picking were related. The data suggested that the complicated and fine work of nut cracking forces the chimpanzees to control their fingers and hands extensively. The task facilitates specialization and coordination in using their hands. Human handedness may have emerged through the learning process of complicated skills which required complex and complementary use of the hands. The cognitive ability of each species must have been an important factor, but the kind of task may have decided whether specialization of hand preference developed or not. That is why almost exclusive laterality in hand use develops only in certain particular behaviors, such as nut cracking, whereas only weak laterality develops in certain other behaviors, such as food picking.

Nut cracking by chimpanzees using a hammer-anvil pair is one of the most advanced and complicated tool-using behaviors known among nonhuman primates (BOESCH & BOESCH, 1984; SAKURA & MATSUZAWA, 1991). This behavior requires the coordination of both hands and recognition of the relation among at least three components: the anvil stone, the nut to be cracked, and the hammer stone. The recent finding of meta-tool use shows that chimpanzees can even employ a fourth component, a wedge stone, to keep the anvil stone flat and stable (MATSUZAWA, 1991b). It thus takes a long time for chimpanzees to learn skillful techniques. At Bossou, there are still two adult chimpanzees and a 7-year-old female who do not perform nut cracking. The above facts clearly demonstrate that successful performance of this behavior requires long-term learning and that some chimpanzees fail to learn.

During the learning process of nut cracking in juveniles and adolescents, some chimpanzees attempt to hold the hammer just in one hand and then the other; that is, they change the hand that holds the hammer. However, the chimpanzees eventually come to use only

one hand exclusively. The fact that three out of six kin-related pairs were opposite-hand users also suggests that the learning process rather than genetic factors plays an important role in the development of exclusive hand use in nut-cracking behavior.

However, the hand used in hammer holding was positively correlated with the hand used in food picking. This suggests that an individual genetic bias towards left or right may also affect the development of hand preference. To elucidate the genetic traits of hand preference, we are attempting to identify the biological father of each young individual by DNA-typing analysis (SUGIYAMA et al., in press).

Taking the above findings together, we postulate that the long-term learning process may amplify an inherent tendency for hand preference and, in some cases, may result in an exclusive hand preference. Fine manipulation with the fingers, control of the power of the hand holding a hammer, and use of one hand for the hammer and another for nuts, require functional specialization of each hand. Once specialization has been acquired, it would increase the learning efficiency, and create a positive feedback loop of learning. To confirm the above hypothesis, other tool-using behaviors of chimpanzees must also be investigated in terms of hand preference. Fine-stick manipulation for fishing termites, hard-stick use for digging termite-mounds, and long-wand use for ant-catching (SUGIYAMA, 1993) are available as candidates.

We can regard the hand preference observed in nut cracking by chimpanzees as comparable to that of human beings in terms of its exclusiveness. However, the laterality at the population level is different between the two species: 95% of human beings are right-hand users, while the Bossou chimpanzees did not show a right-hand bias. In conclusion, human right handedness at the population level had no counterpart in chimpanzees who showed exclusive hand preference at the individual level.

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