International Journal of Primatology, Vol. 12, No. 6, 1991

Handedness in Wild Chimpanzees

Christophe Boesch[1,2]

Received January 28, 1991; accepted February 22, 1991

The debate over nonhuman primate precursors to human handedness is unsettled mainly due to lack of data, particularly on apes. Handedness in wild chimpanzees at the Tai National Park, Cote d'lvoire, has been monitored in four tasks. For the simple unimanual ones, reaching and grooming, adults use both hands equally (ambidextrous), while for the more complex unimanual wadge-dipping and the complex bimanual nut-cracking, adults are highly lateralized. These results support the hypothesis that lateralization increases with the complexity of the task. The lateralization is constant for years for each task but may vary in an individual with respect to different tasks. For nut-cracking, females are more lateralized than males. The ontogeny of handedness for nut-cracking shows many variations in the tendency to use one hand and in the side preferred, until at about 10 years of age, the individual achieves her adult handedness. No population bias toward one side exists in Ta'i chimpanzees. No heritability of handedness between mother and offspring was observed. Human and chimpanzees handedness are compared.

KEY WORDS: chimpanzees; handedness; laterality; ontogeny; heritability.

INTRODUCTION

Manual specialization is often considered to be the first step in the evolution of left-hemispheric specialization of the brain in *Homo sapiens* (MacNeilage *et al,* 1987). However, right handedness is not universal in modern humans, since about 10% of people show a strong left-hand preference, and about 30-40% show at least one left-hand preference when

[1]Ethology and Wildlife Research Department, University of Zurich, Zurich, Switzerland.
[2]Present address: Institute of Zoology, University of Basel, Rheinsprung 9, 4051 Basel, Switzerland.

several actions are considered (Annett, 1987). Tool use or aimed throwing has been proposed as the adaptive force that led to such a manual inequity (Calvin, 1987; Corballis, 1983, in MacNeilage *et al.,* 1987). As both behaviors are observed in wild chimpanzees, an incipient specialization between the hands may exist in them and other primates.

Precursors to human handedness patterns in nonhuman primates have been debated between those who advocate its presence and others who deny them any hand preference. Most results, which have been obtained in experimental settings with monkeys, led to the clear conclusion that non-human primates do not have human-like handedness (Warren, 1980, 1987). MacNeilage *et al.* (1987) have challenged this interpretation by proposing that the apparent lack of handedness was due to the mixture of two different types of manual specialization in nonhuman primates: first, a higher left-hand preference for visually guided tasks, such as simple prehension of objects and, second, a right-hand preference for manipulatory tasks. However, the reconsideration of previous data and some new data offered were not conclusive in one direction or the other, and more information is badly needed (MacNeilage *et al.,* 1987). This is particularly true for the apes, which could be intermediate between monkeys and humans (Nishida and Hiraiwa, 1982; Marchant and Steklis, 1986).

Published data are even more limited for ontogenetic aspects of handedness. Data on only a few individuals are available for some species of primates, which do not allow generalization at the specific level (Bresard and Bresson, 1983; Fagot and Vauclair, 1991). In humans, the degree of hand preference seems more readily inherited than the direction of handedness (Bryden and Steenhuis, 1987).

I present here observations on handedness in a community of wild chimpanzees on 4 spontaneous manual tasks, while they foraged in their natural environment. For the analysis, I consider the following four hypotheses on handedness: the nonlaterality (Warren, 1980), the shifting lat-erality (MacNeilage *et al.,* 1987), the human-like right handedness, and one stating that hand preference increases with the level of complexity of the task presented to the subject. For the last hypothesis, data on different tasks were collected from the same individuals in order to test whether there is an increase in laterality.

METHODS

We started the long-term study on chimpanzees of the tropical rain forest in the Tai National Park, Cote d'lvoire, in September 1979. No artificial provisioning was used and full habituation was a slow process over about 5 years. Since March 1984, we have been able to follow the chimpanzees at close range throughout their daily foraging. The community lives in a 27-km^2 home range in the western part of Tai N.P. The membership has declined from 80 to 60 individuals, due to many disappearances, births, and transfers. Boesch and Boesch (1983, 1984b) published details on the habitat, the habituation process and the data collecting methods.

Manual activities were recorded as a routine procedure for nut-cracking behavior (Boesch and Boesch, 1983, 1984a, b). I analyzed hand preference using three measurements: (a) one hand-use, the tendency to use one hand instead of both together (only for nut cracking); (b) laterality, the tendency to use one hand more than the other, ranging from 50 to 100%; and (c) right-hand preference, the tendency to use the right hand. In order to follow variations in hand preference, I recorded hand use in three additional tasks with different levels of complexity, from September 1989 to October 1990.

The manual tasks studied are as follows.

(1) *Reaching:* The simplest reaching task could be observed in the consumption of certain species of fruit *(Parinari excelsa, Sacoglottis gabonensis, Irvingia gabonica,* or *Nauclea xanthophyllon).* The chimpanzees collect two handfuls of fruits, sit down, and place them on the ground in front of them. To extract the juice, they reach out and pick up one fruit after the other, bite away the fruit flesh, and chew it extensively into a wadge. They discard it by letting it drop into their hand and then put it on the ground. As the chimpanzees are free to choose the place and position to sit in the forest, I consider this task to reveal unbiased hand preference for *a simple one-handed task.* For each reach toward a fruit I recorded the hand that was used to take it. For the present analysis, I considered only individuals for which I had collected 7 or more observations, viz., 20 adults (6 males with an average of 122 observations and 14 females with an average of 22 observations).

(2) *Grooming.* Social grooming involves at least two individuals. The task requires the groomer to sweep the hair of the groomee with one hand, in order to expose the skin underneath and to remove dirt particles and parasites. This can be done by using both hands. However, frequently only one hand is used while the other one either holds on to a nearby branch or rests on the ground. With the latter cases, I recorded the hand used to groom and entered a new data point each time the groomer changed posture or whenever the unimanual grooming session had been interrupted by a bimanual sequence. For grooming, the groomer is, to a certain extent, restricted in its choice of the place where the session takes place, as well as in the choice of grooming hand. Indeed, the goal is, most reciprocally, to groom another individual, which sits in a given place, and the grooming

hand depends on the areas to be groomed. So it represents a *simple one-handed task with some external constraints.* I considered for this analysis only the individuals on which I had collected seven or more observations, i.e., 14 adults (6 males with an average of 119 observations and 8 females with an average of 22 observations).

(3) *Wadge-Dipping:* After collecting handfuls of fruits of *Sacoglottis gabonensis,* and bringing them to a water puddle, they chew them to pro duce wadges that they dip repeatedly in the water with one hand. The sub ject removes the wadge from its mouth, dips it in the water, and brings it back to its mouth (three movements). They may feed at the same place for more than 30 min, dipping the wadge approximately every 2 min. All observed individuals consistently used the same hand at the same place. Therefore, I entered only one data point for each session of fruit consumption at the same puddle in the same sitting posture. Whenever an individual changed position at the puddle or moved to another one, I entered a new data point. The chimpanzee is free to choose the position and place to sit near a puddle, and I consider this task to reveal the hand preference for a *one-handed task of three movements.* For this task, I could collect 7 or more observations with 18 adults (6 males with an average of 52 observa tions and 12 females with an average of 15 observations).

(4) *Nut-Cracking:* In order to eat five species of nuts, the chimpanzees collect them, place them one by one on an anvil, usually a root, and pound them with a hammer, which is either a fallen branch or a stone (Boesch and Boesch, 1983). Nut-cracking is a complex task, involving both hands and often also the feet (for holding the nuts or the hammer); the anvil is cleaned of the remains of previously cracked shells and the nut is then placed on the anvil and pounded. Once open, while one hand holds the hammer, the other brings the kernel to the mouth. The pounding itself consists in a series of rapid powerful movements. If they occur, corrections in the trajectory or the power of the hits are performed extremely quickly, without interrupting the pounding movement. When cracking the nuts in trees, one hand supports the target nut all the time in order to prevent it from bouncing away. Because hammers are of different weights and sizes, chimpanzees may be forced to use both hands to hold the large ones and to control their strength for precise amounts of force. With small hammers, adults consistently use only one hand. Some individuals may bias their choice toward smaller hammers in order to use one hand only. We gave one data-point entry for the use of either one hand or both during a nut-cracking session, i.e., when cracking nuts with the same hammer at the same anvil, independent of the number of transports made to gather nuts and the number of nuts eaten (duration of sessions vary from 4 min to 3 hr). Adults were quite constant in their hand use, and any changes were

from one to both hands (giving two data-point entries). They never changed from one hand to the other. However, juveniles and infants were much less stable in their hand preference so that we counted the number of nuts opened when using one or both hands or even the number of hits given with one or both hands for infants too young to succeed in opening a nut. I consider nut-cracking to be a *complex bimanual task,* for which I recorded the hand holding the hammer. For this task, 7 or more observations were collected on 45 adults (13 males with an average of 48 observations and 32 females with an average of 38 observations), 13 adolescents (4 males and 9 females), and 27 juveniles and infants ranging from 1 to 9 years old. Most individuals were followed for 2 to 5 years.

According to the four hypotheses for explaining laterality in nonhu-man primates, the predictions are obvious for that of nonlaterality (no hand preference) and the human-like right-hand preference (right hand use in 90% of the individuals), but more difficult for the two others. The shift-ing-laterality hypothesis predicts left handedness in reaching, wadge-dipping, and possibly grooming, as these are simple but visually guided tasks, and right handedness in nut-cracking for the more demanding manipulatory task of pounding. The increasing-complexity hypothesis predicts no laterality (an ambidextrous pattern) in reaching, but a high hand preference in nut-cracking, with wadge-dipping and grooming being intermediate.

RESULTS

Handedness in Adults

Handedness might be subject to a maturation process and vary according to the age of the individual. We, therefore, first consider handedness in adults and then look for the maturation of this phenomenon.

Laterality

Figure 1 shows, for the four tasks, the tendency of adults to use one hand more than the other one. Table I contains all data on adults, with a binomial z-score for each task, to determine whether there is a significant deviation from chance distribution. For the two simple unimanual tasks, adults seems to be ambidextrous: in reaching, only 10 individuals of 20 (chi-square goodness-of-fit test $x^2 = 0.00$, df = 1, ns), and in grooming, only 5 individuals of 15 ($x^2 = 1.66$, df = 1, ns) possess a hand preference above chance level. Whereas for the two more complex tasks, wadge-dip-

Table I. Data on Individual Hand Preference in Adults of the Taï Chimpanzee Community[a]

Name	Reaching			Grooming			Wadge-dipping			Nut-cracking			
	N	R	*Z*	*N*	R	*Z*	*N*	R	*Z*	*N*	H	R	*Z*
Adult males													
Brutus	71	53	0.47	112	61	2.07	30	100	5.29	61	55	76	2.91
Darwin	141	47	0.67	53	60	1.37	50	42	0.98	138	84	96	9.98
Kendo	145	53	0.83	157	63	3.19	48	100	6.78	60	96	100	7.48
Macho	226	30	5.64	139	58	2.03	79	100	8.77	67	64	88	4.87
Rousseau	60	5	6.84	41	46	0.31	24	0	4.69	27	59	100	3.75
Ulysse	92	63	2.39	214	48	0.34	80	100	9.05	93	50	8	5.54
Balzac										10	80	75	1.06
Falstaff										38	76	31	1.85
Chinois										30	83	20	2.80
Pistache										11	54	33	0.40
Schubert										14	71	20	1.58
Snoopy										57	75	4	5.79
Wotan										20	80	81	2.25
Adult females													
Bijou	49	40	1.14	7	100	2.26	22	22	2.34	51	82	0	6.32
Ella	10	40	0.31	19	47	0.00	13	100	3.32	68	86	88	5.72
Goma	21	71	1.74	18	61	0.70	20	100	4.24	118	75	100	9.32
Malibu	15	80	2.06	10	50	0.31	8	0	3.18	68	79	5	6.39
Mystère	12	36	0.86	43	69	2.43	12	41	0.28	40	87	0	5.74

Ondine	54	55	0.58	37	54	0.32	45	100	6.55	77	85	100	8.00
Cannelle										14	64	100	2.66
Fanny	7	0	2.26							30	86	88	3.72
Gala										20	50	100	2.84
Gauloise										32	96	100	5.56
Gitane	37	48	0.00	7	85	1.51				38	21	0	2.47
Héra	32	65	1.59				7	0	2.26	87	83	4	7.72
Kiri	25	60	0.80							60	26	12	2.75
Lola										11	36	50	0.50
Loukoum	57	70	2.91				11	100	3.01	41	80	3	5.22
Marlène										27	66	94	3.53
Momo										19	52	10	2.21
Nova										19	57	100	3.01
Perla				31	47	1.43	14	100	3.47	34	85	0	5.19
Pokou										17	88	6	3.09
Poupée	39	33	1.92	23	47	0.00				50	69	0	5.65
Ricci	18	100	4.00							50	96	100	6.78
Salomé	22	27	1.91				30	66	1.64	106	41	0	6.48
Saphir										25	44	100	3.01
Tosca										16	81	0	3.32
Véra										14	64	88	2.66
Xérès										63	78	2	6.78
Zoé										14	85	0	3.17

[a] N = number of observations, R = right-hand preferencce (%) (see Methods for further explanations); Z = binomial z score (values over 1.65 are significant at $P < 0.05$ and values over 2.33 at $P < 0.01$); and H = one-hand use.

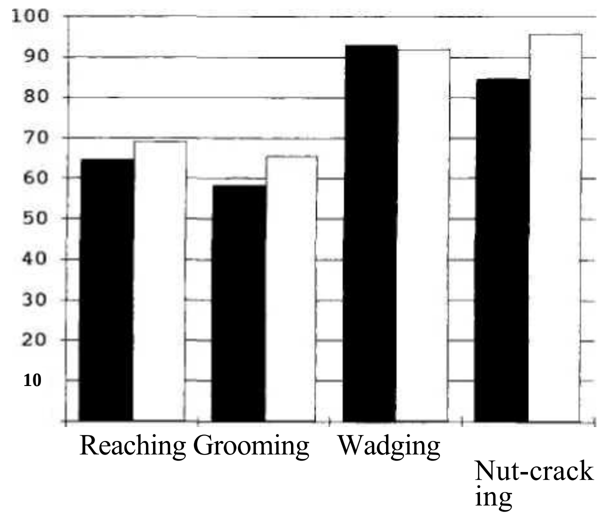

Fig. 1. Laterality (in %) in four tasks by adults in Tai chimpanzees.

ping and nut-cracking, the sexes are more lateralized [for wadge-dipping 13 individuals of 16 have a hand preference (x^2 = 6.25, df = 1, P < 0.05) and in nut-cracking 37 individuals of 41 have one (x^2 = 26.56, df = 1, P < 0.001)]. The commonly used criteria of using the same hand in 70% of the observations (MacNeilage *et al,* 1987) is exceeded for wadge-dipping in most adults (chi-square goodness-of-fit test significant at P < 0.05 in 11 of the 16 adults), as well as for nut-cracking (chi-square goodness-of-fit test significant at P < 0.05 in 30 of the 41 adults).

Table II. Age and Sex Differences in Lateralization (or Hand Preference) for Nut-Cracking in Tai Chimpanzees"

	Hand lateralization		
	100%	Above 70%	Under 70%
Adult males	2	5	6
Adult females	16	7	5
Adolescent males	2	2	—
Adolescent females	8	1	—
Juvenile males	3	—	4
Juvenile females	4	—	—
Infant males	3	2	8
Infant females	1	—	6

"To be considered above the 70% criterion, the individual performance should significantly exceed it.

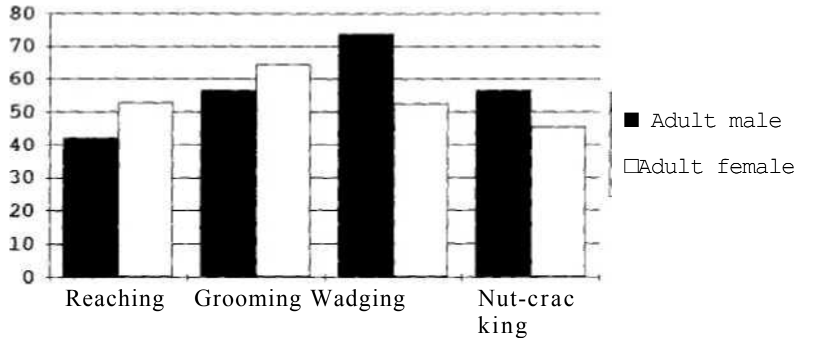

Fig. 2. Right-handedness (%) in four tasks by adult male and female Tai chimpanzees seen performing one or more of them.

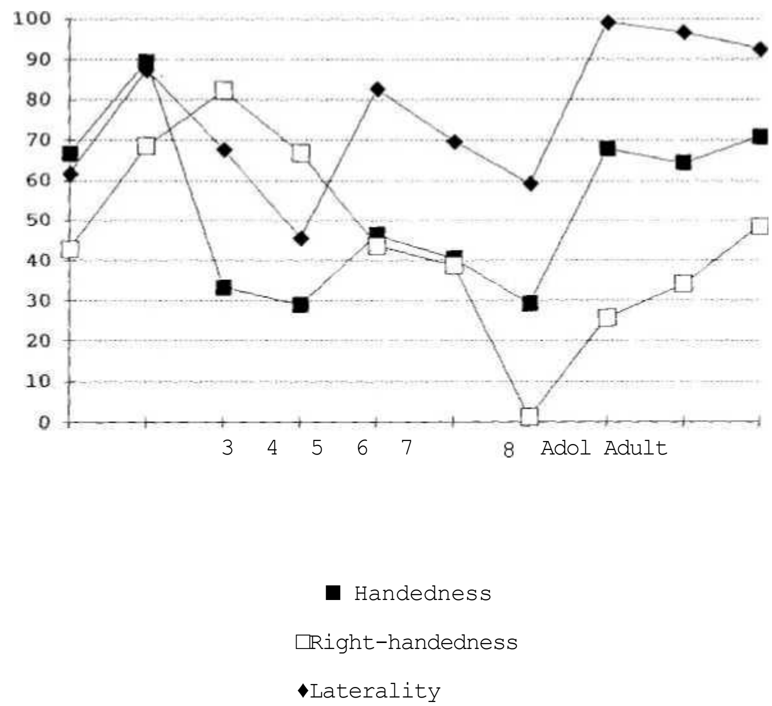

Fig. 3. Variation in handedness (%) for nut-cracking during the ontogeny of Tai chimpanzees.

Table III. Ontogeny of Handedness in Nut-Cracking in Taï Chimpanzees[a]

Subject	Age (years) 1	2	3	4	5	6	7	8	9	
Brando		100/50		63/76	56/97					Increase
		(160)		(33)	(2723)					
Kana	100/85	85/96								Increase
	(70)	(557)								
Nino	0/–									—
	(238)									
Popeye	100/100									—
	(31)									
Gallus		95/100								—
		(57)								
Goshu		96/34	51/25							Decrease
		(363)	(672)							
Orée		100/100	40/100	0/–						Same
		(13)	(1396)	(152)						
Rubis		51/100	47/100							Same
		(57)	(392)							

Xindra	100/0 (20)		100/100 (31)	0/– (193)					Reversal
Goyave		34/90 (415)	12/47 (2355)						Decrease
Kummer		0/– (21)	40/98 (131)						—
Lychee		25/78 (218)							—
Marius		68/100 (98)	0/– (7)	100/0 (3)	0/– (7)	0/– (17)			Reversal
Zorba		0/– (293)							—
Eros			0/– (30)	0/– (32)	6/100 (187)				—
Molière			0/– (88)		43/100 (30)				—
Nina			5/78 (1211)						—
Sartre			0/– (16)	36/0 (61)	26/27 (274)	9/– (9)	69/3 (45)	5/0 (146)	Variable
Tarzan			98/3 (257)	21/2 (3251)					Same

Table III. Continued

Subject	Age (years) 1	2	3	4	5	6	7	8	9	
Ali					50/0	0/–	60/3	52/0	66/11	Same
					(14)	(154)	(253)	(29)	(332)	
Azur					14/100					—
					(7)					
Chouchou					100/0	78/0	75/0			Same
					(3)	(14)	(4)			
Gérald					100/81	99/44				Decrease
					(195)	(5187)				
Gipsy					100/0	79/0		35/0	13/0	Same
					(71)	(79)		(35)	(13)	
Lolita					9/100	75/0	11/0			Reversal
					(83)	(158)	(87)			
Négus					17/100					—
					(6)					
Cléo								62/00	75/100	Same
								(8)	(8)	

[a]For each individual are given, for each year, first the tendency to use one hand (%) and then the right-hand preference (%). Underneath are given (in parentheses) the total observation time. Individuals seen only to crack nuts with both hands are marked with –. In the last column is the direction of significant changes in hand use across the years.

Adults of both sexes have the same tendency to use one hand except for nut-cracking, in which males are less lateralized (Mann-Whitney U-test: nut-cracking, z = 3.43, *n1*=- 13, *n2 = 32,P*< 0.001). Both sexes are equally ambidextrous for reaching (R) and grooming (G) (Mann-Whitney U-test: $P > 0.05$) but present an increasing tendency to use the same hand when wadge-dipping (W) or nut-cracking (N) (Mann-Whitney U-test: $P < 0.05$). However, the lateralization is the same for nut-cracking and wadge-dipping in both sexes (Mann-Whitney U-test: male N/W—z = 1.84, $P > 0.05$; female N/W—z = 0.24, $P > 0.05$) (Fig. 1). A similar comparison, including only the individuals for which we have enough observations on all four tasks (six males and six females) confirms these results: grooming and reaching are less lateralized than wadge-dipping and nut-cracking [Friedman two-way analysis of variance by ranks—$N = 12$; laterality—$F = 13.82$, $P < 0.01$; and multiple comparisons between tasks—$P < 0.05$ (Siegel and Castellan, 1988)].

For nut-cracking, lateralization remained constant for years, and long-lasting changes occurred only when a wound prevented an individual from using its preferred hand, as observed for one male and one female. Both subjects switched back as soon as they could use their preferred hand again. Some individuals have a more ambidextrous tendency, for example, switching hands if they have to sit in a position to pound on a root anvil with their usually preferred hand very close to the tree trunk, and also while using bigger, sometimes stone hammers. Per contra, other subjects consistently used the same hand regardless of technical problems encountered when cracking nuts (Table II). More adult females than males possess 100% lateralization (criteria of 100% versus <100%: $x^2 = 6.28$, df= *1,P<0.05).*

Hand Preference

Consistency in the direction of hand preference, when stable over the years for one task, was observed to remain stable over the four tasks in only 8 of the 12 individuals for which I have enough data on the four tasks. Three individuals present a reversal in hand preference for one of the tasks [for a reversal to occur the side of the hand preferred (criterion of 70% significantly exceeded) has to shift from one hand to the other one for one of the four tasks] and another subject exhibited a reversal in two tasks. Thus, if the individual hand preference remained constant for years for a specific task, it seemed less constant for different tasks.

Tai chimpanzees, which have a hand preference, show no population bias toward one side; half of them are right-handed *[P* > 0.05 for all individuals (Fig. 2) or for the 12 individuals observed in all four tasks; Friedman two-way analysis of variance by ranks; $N = 12$, right handedness; $F = -2.52$, $P > 0.05$].

Ontogeny of Handedness

Laterality

We have data only on nut-cracking behavior (Table III), in which the youngsters' hand preference could be influenced by the size and/or weight of the hammer, which may force them to use both hands. In Fig. 3, it appears that the use of a single hand is unstable (handedness in Fig. 3: $x^2 = 65.27$,[3] df = 4, $P < 0.001$). At the beginning, it is very high. Trials during the first 2 years are often inappropriate: young infants may hit the nuts directly with the bare hand or with very small hammers or pound the nuts on the ground instead of on an anvil or merely pound an anvil without a nut. Such pounding without a hammer or the use of ineffective hammers may explain the very high proportion of unimanual nut-cracking in the youngest chimpanzees. Single hand-use decreases as the infants begin to use their mothers' hammers, which are quite heavy and force them to use both hands in order to increase their strength to manipulate them (Fig. 4). Later it increases again as they gain enough strength to manipulate heavy tools with one hand.

The tendency to use only one hand for nut-cracking varies greatly during the apprenticeship of the technique [laterality in Fig. 3 (as above with only the first-year data point for each individual): $x^2 = 37.49$, df = 4, $P < 0.001$], but in an irregular way. This illustrates the instability of the youngsters which, when encountering technical difficulties in opening a nut, try to solve the problem by alternating many times between hands to hold the hammer and pound the same or other nuts. Such permutation in the hand used are observed until the age of 7 years.

Hand Preference

Right-handedness is very high during the first years of nut-cracking; it reverses for the intermediate period; and then stabilizes at the adult level [right-handedness in Fig. 3 (test performed as above): $x^2 = 27.07$, df = 4, $P < 0.001$]. These variations are puzzling. However, no individual was fol-

[3]The chi-square test is performed only with the first-year data point for the same individual to assure independence of the data, as most individuals were observed for many years and contributed to more than one year. However, this procedure reduced the sample; therefore, it was possible to make the test only for the first 5 years, for which N ranges from 3 to 7.

Fig. 4. A 3-year-old female tries to crack a nut with the medium-sized wooden hammer used by her mother. In a movement typical for her age, she gets up while lifting the hammer in order to be able to control the pounding movement and to achieve a bigger amplitude to hit. Unlike adults, youngsters do not have the strength to lift a hammer of that size with one hand, which explains the high proportion of bimanual pounding in 3-year-old infants.

lowed long enough to provide data both before and after the bimanual period. This, plus the fact that the 7- to 8-year sample is rather small ($N = 5$ and 4, respectively, in Table III and Fig. 3), prevents us from drawing conclusions about this apparent shift in hand preference. Analysis of hand preference over 2 successive years on the same individuals (Table IV) shows that for infants under the age of 5 years ($N = 11$ individuals), significant variations in the use of one hand ($P < 0.05$) tend to be more frequent than for subjects between 5 and 9 years old ($N = 10$ individuals), though this is not significant (Fisher exact probability test: $P > 0.05$). Two of the three reversals observed after 5 years of age were actually only a marked increase in the use of the same hand, and not a shift from one side to the other. In all unclear cases, the infant did not crack nuts unimanually for some of the years.

Table IV. Important Variations in Hand Preference Observed in Youngsters Between Two Consecutive Years During Ontogeny[a]

	2 to 5 years	6 to 9 years
Present	6	3
Absent	3	4
Unclear	2	3

[a]Variation is important when a chi-square test is significant at $P < 0.05$.

Heritability

The likelihood of using one hand and the extent to which it is used are factors that could be transmitted genetically or socially between mothers and infants. In Table V, I compare these two factors for mother/infant pairs with those for adult females/infants. If similarity is higher for laterality than for right-handedness in both comparisons, no statistical tendency between the mother and her infant is apparent in our sample. However, some striking cases show that imitation plays a role in the acquisition of some aspects of hand use. For example, Ella has a strong right-hand bias, but one of her three sons exhibits a strong left-hand bias. Of the two others, which, like her, are strongly right-hand biased, the older has developed the habit of holding hammers at the right extremity above the ground with his right foot to support his right hand. He was the only chimpanzee in the study community to do this until his youngest brother rigidly adopted this way of holding the hammer.

DISCUSSION

Observations of ontogenetic changes of hand preference in Tai' chimpanzees are preliminary but clearly demonstrate the care that is needed to consider data from subadult subjects because they may not reflect adult performances. Previous studies on subadult subjects (MacNeilage *et ai*, 1987) may have distorted our understanding of primate handedness. Further, the frequent reversals in hand preference for different natural tasks by the same individuals among Tai chimpanzees may explain some of the inconsistencies found in captive studies, in which handedness is analyzed for different tasks under different conditions and on individuals of different ages and species.

Table V. Similarity in the Degree and Direction of Hand Preference for Nut-Cracking in Tai Chimpanzee Infants 5 Years and Older with Their Mothers, as Well as for the Same Infants with All Adult Females of the Community, Excluding Their Mothers"

	Infants-mothers	Infants-females
Laterality	0.609	0.630
Right-handedness	0.419	0.309

"A coefficient of similarity was used, which is between 1.0 (100% similarity) and 0.0 (no similarity). Statistical comparisons between the coefficients of similarity are made with the Wilcoxon signed-ranks test (— = $P > 0.05$, * = $P < 0.05$; ** = $P < 0.001$).

Of the four hypotheses considered to explain handedness in primates, only the increasing-complexity hypothesis seems to be supported by my results. However, if the high lateralization observed during nut-cracking could be expected from the tool-use as a precursor-of-handedness theory (Corballis, 1987) or the complexity hypothesis, it is surprising that wadge-dipping presents a level of manual specialization similar to that of nut-cracking. Although wadge-dipping can be separated into three movements (taking from the mouth, dipping in water, and bringing back to the mouth), reaching seems not to be complex and is not comparable to the motor skills implied by hammering.

It is noteworthy that an individual eating fruits of *Sacoglottis* under a tree may reach ambidextrously for them when sitting away from a puddle but be strongly lateralized some minutes later if it sits near a puddle and dips wadges. This may reflect a basic hand preference for an easy multiple movement with a longer duration than simple reaching. This would support the complexity hypothesis even though we should understand complexity in a broad sense (simple versus multiple movements). No community bias toward a preference for either hand is observed in the Tai chimpanzees.

Like Tai chimpanzees, individual humans in a population exhibit variations in the degree of use of the preferred hand for different tasks, and they may be totally ambidextrous for certain simple unimanual tasks, including picking up a penny, pointing, snapping one's fingers, picking up a glass, turning on a light switch, and crumpling a piece of paper (Bryden and Steenhuis, 1987). The latter suggests the possibility that the complexity of tasks might also play a role in the degree of laterality in humans.

Unlike humans, in chimpanzees handedness requires many years before it is durably established, seems not to be inherited, and presents no population bias toward the right hand. Like humans, in chimpanzees lateralization is a function of the task considered and can be extremely marked and stable for years. Thus, in Tai chimpanzees, clear hand preferences exist but the phenomenon seems to be different from that of humans in some features.

ACKNOWLEDGEMENTS

We thank the "Ministere de la Recherche Scientifique" and the "Min-istere des Eaux et Forets" of Cote d'lvoire for permitting this study and the Swiss National Foundation, the L. S. B. Leakey Foundation, The Schultz Foundation, and the Jane Goodall Institute for financing it. This project is integrated in the UNESCO project Tai-MAB under the supervision of Dr. Henri Dosso. We are most grateful to A. Aeschlimann, F. Bourliere, and H. Kummer for their constant encouragement. We thank Kim Bard and Bill McGrew for commenting on the manuscript. P. and B. Lehmann, L. and E. Ortega, directors of the CSRS in Abidjan, for their efficient logistic help, and T. Tiepkan of the station IET in Tai for his friendly support in our daily camp life.

REFERENCES

Annct, M. (1987). Handedness as chance or as species characteristic. *Behav. Brain Sci.* 10(2): 263-264.

Boesch, C, and Boesch, H. (1983). Optimization of nut-cracking with natural hammers by wild chimpanzees. *Behaviour* 83: 265-286.

Boesch, C, and Boesch, H. (1984a). Mental map in wild chimpanzees: An analysis of hammer transports for nut cracking. *Primates* 25: 160-170.

Boesch, C, and Boesch, H. (1984b). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *J. Hum. Evol.* 13: 415-440.

Bresard, F., and Bresson, F. (1983). Handedness in Pongo and Pan troglodytes. *J. Hum. Evol.* 12: 59-66.

Bryden, M. P., and Steenhuis, R. E. (1987). Handedness is a matter of degree. *Behav. Brain Sci.* 10(2): 266-267.

Calvin, W. (1987). On evolutionary expectations of symmetry and toolmaking. *Behav. Brain Sci.* 10(2): 267-268.

Fagot, J., and Vauclair, J. (1991). Manual laterality in nonhuman primates: A distinction between handedness and manual specialization, *Psychol. Bull.* 109(1): 76-89.

MacNcilage, P., Studdert-Kennedy, M., and Lindblom, B. (1987). Primate handedness reconsidered. *Behav. Brain Sci.* 10(2): 247-263.

Marchant, L. F., and Steklis, H. D. (1986). Hand preference in a captive island group of chimpanzees *(Pan troglodytes). Am. J. Primalol.* 10: 301-13.

Nishida, T., and Hiraiwa, M. (1982). Natural history of a tool-using behaviour by wild chimpanzees in feeding upon wood-boring ants. *J. Hum. Evol.* 11: 73-99.

Siegel, S., and Castellan, N. J. (1988). *Nonparamelric Statistics for the Behavioral Sciences,* McGraw-Hill, New York.

Warren, J. M. (1980). Handedness and laterality in humans and other animals. *Phys. Psychol.* 8:351-359.

Warren, J. M. (1987). Primate handedness: Inadequate analysis, invalid conclusions. *Behav. Brain Sci.* 10(2): 288-289.