SPONTANEOUS HAND USAGE AND HANDEDNESS IN A TROOP OF BABOONS

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INTRODUCTION

In his discussion of hemispheric laterality, Denenberg (1981) proposes to distinguish between brain lateralization at the level of the individual animal and that at the level of the species or population. He goes on to state that if a population is lateralized, then the individuals which compose that population will necessarily be lateralized too. The converse, however, is not always true; this is exemplified by the case of nonhuman primates. In the several primate species tested (e.g., Finch, 1941; Warren, 1953; Brookshire and Warren, 1962; Kawai, 1967; Tokuda, 1969; Lehman, 1970, 1978a, 1980a; Brooker et al., 1981) no preferential bias was found for the population, even though some individuals were strongly lateralized (to the right or to the left). In accordance with Denenberg, one can hypothesize that evidence of lateralization at the population level indicates the action of evolutionary processes. Now, if the population, as such, is not lateralized, the role of selective pressure becomes less obvious and the necessity to search for other factors arises (for example those at work at the individual level). Among these individual factors, the more commonly studied are genetic kinship, sex, age and experience.

A brief survey of the literature on monkeys (which is primarily concerned with the genus macaque) provides the following picture: genetic kinship (mother-offspring and between offsprings) doesn't predict laterality (e.g., Brooker et al., 1981); furthermore, the choice of the preferred hand doesn't depend on the sex (e.g., Lehman, 1978a, 1980a); however it appears from systematic studies on macaques, that hand preference is influenced by the age of the monkeys: adult macaques appeared to be more strongly lateralized than the young (Lehman, 1970, 1978a, 1980a; Brooker et al., 1981). This latter result calls for an explanation in terms of an acquisition of preferential bias in macaques, and the possible role of external stimuli in this acquisition.

When one considers the effects of the nature and of the repetition of tasks on handedness, results are somewhat equivocal. The bias which develops for a novel task is not very predictive of future preferences

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(Warren, 1980); however practice with the same task leads to strong preferences (Ettlinger, 1961). When different manipulatory tasks are carried out by the same animals, a slight bias seems to emerge for similar tasks (Brookshire and Warren, 1962; Beck and Barton, 1972), but inversions of preferences have also been observed as a function of the tasks considered (Deuel, 1975). The choice of the hand is also determined by the position of the object, since monkeys tend to use preferentially the hand nearer the object (Cronholm et al., 1963; Lehman, 1978b, 1980a).

From this set of results, one could temporarily conclude with Warren (1980) that the generalization of manual preference across different tasks is limited and that such a generalization might be dependent on several variables (e.g., the type of task, past experience).

The aim of the present study is to obtain informations on hand use in a troop of Guinea baboons. This species has not, to our knowledge, been tested for its preferential biases; a few reports (Butler and Francis, 1973; Trevarthen, 1978) have studied manual activities in baboons, but their primary goal was not an investigation of laterality. The hand of the baboon has interesting features: according to Napier and Napier (1967), Papio species have an index of opposability (between thumb and index) of 57, the closest to man (man: 65; chimpanzee: 42; macaque: 54). On these morphological grounds and on other grounds (cf. the high levels of manipulatory activity observed in these animals, Joubert and Vauclair, 1986), the baboon should represent a good candidate for an analysis of manual activities. The work reported here is based on observation of all actions involving one or both hand(s); thus all manual actions with partners, physical objects and self-directed activities are recorded. The troop lives in semi-natural conditions (in a large enclosure) and the baboons have no physical contact with humans: for example, they never receive food directly from the hand of the keeper or observers.

The specific aims of our study are firstly to quantify hand uses in several spontaneous activities. Secondly, since the troop is divided into two main age classes, special attention will be given to the comparison between young and adults in terms of measure of handedness (preference and strength) and position of objects under manipulation.

Materials and Methods

Subjects

Eighteen Guinea baboons (*Papio papio)* living in an enclosure were studied. The group comprised ten adults (five males and five females) each about 7 years old, and their offspring (N = 8), infants or juveniles (5 males and 3 females),

ranging from 7 to 32 months of age. All adults were born in the wild, and were brought to their present enclosure in 1980. All the young animals were born in captivity.

Living Conditions

The enclosure was a rectangle of 30 m × 25 m. It contained a dead tree, rocks of various sizes and a wooden construction (4.5 m high). At regular intervals different kinds of branches were brought into the compound. A tunnel connected the compound to the animal house (a concrete building of 4 m × 3 m) and the animals were able to move freely from one to the other. Food (special monkey chow, carrots, apples and bananas) was always given in the enclosure.

Procedure

Behaviours were recorded from an observation tower located in a nearby tree. Each subject was videotaped for a total of 40 min (eight daily sessions of five min each). A frame by frame analysis of the tapes allowed the recording of all unimanual and bimanual activities. Only those behaviours allowing free movement of the hands (that is when the animals were seated) were considered.

Only occurrences of behaviours were recorded, independently of their duration. Moreover, an ongoing behaviour which was interrupted for more than 1 sec was counted as having occurred twice. Since the behavioural categories were mutually exclusive (see coding system below), it was then possible to code appropriately a sequence of manual acts.

Coding System

Unimanual activities (UA) have been coded with respect to (a) the position of the object before it was manipulated: in front of the subject, ipsi- or contralateral to the hand used, (b) the choice of the hand (right or left).

We have considered two categories of activities involving both hands: (a) bilateral bimanual activities (BB) described simultaneous, symmetrical actions of the hands; (b) asymmetrical bimanual activities (BA) were defined as the differenciated action of the two hands. Following suggestions made by Napier (1961) and Reynolds (1975), it appeared to us that an index of laterality for BAs activities could be derived after consideration of different precision's levels in the prehension. For example, it seems rather plausible that in a bimanual activity of prehension, the preferred hand would perform the most precise movement of the fingers, whereas the non dominant hand would have a supportive role which would involve less differenciation and accuracy in the fingers (Beck and Barton, 1972). We thus categorized prehensibility in a three-level scale: level 0 (the lowest) only involved a global movement of the hand (e.g. leaning the hand against a rock); level 1 described palmar prehension and level 2 implied the differenciated use of fingers as for example the movements of the fingers adopted in precision grip. It was then hypothetized that lateral preference in asymmetrical activities could be attributed to the hand which effectuated the highest level of prehension. This distinction then made possible a comparison of BA activities where prehension of both hands was of the same level and those of different

levels. The position of the object was not coded for bimanual actions, because in such cases the field of manipulations was mostly located in the midsaggital plan (cf. Trevarthen, 1978).

A final step in the analysis consisted of the computation, for each subject, of an index of manual preference (I), using the formula:

$$I = \frac{\text{number of right UAs + right BAs}}{\text{total number of UAs + BAs}} \times 100$$

From this index, we could deduce the preferential bias: a right bias if $I > 50\%$ and a left bias if $I < 50\%$. Furthermore, the strength of laterality was also estimated by applying the simple calculation: $I - 50\%$.

Most of the variables under consideration were analysed using the VAR 3 program (Rouanet and Lépine, 1970) for analysis of variance.

RESULTS

Global Distribution of Manual Activities

A general picture of the distribution of manual activities is provided by Table Ia, which shows the mean percentages of the different categories for age subgroups; Table Ib presents the mean values and standard deviations of all activities for age and sex subgroups.

It is apparent from the data summarized in Table Ib that the subgroup of young was on average more active than the subgroup of adults ($F = 8.00$; d.f. = 1, 14; $p < .025$); but males (as a group) did not differ from

TABLE I

(a) Mean Percentages and Number of All Manual Activities for Each Age Subgroup

	UA	BB	BA	UnKnown	Total
Adults	45.4%	18.4%	24.6%	11.6%	1848
Young	43.4%	25.3%	21.2%	10.1%	2134

(b) Means and Standard Deviations of All Manual Activities for Age/Sexe Subgroups

	Males	Females
Adults	Mean = 178.6 SD = 7.4 N = 5	Mean = 189.4 SD = 9.2 N = 5
Young	Mean = 276.8 SD = 7.7 N = 5	Mean = 252.3 SD = 5.5 N = 3

Note. The category "unknown" contains all behaviours which could not be coded (lack of visibility or uncertainty about definition).

females (F = .02; d.f. = 1, 14; n.s.). Detailed analyses on the effects of age and sex are provided below for separate behavioural activities.

Table Ia further reveals that asymmetrical activities, either performed with one hand (UA) or both hands (BA), represented two-thirds of all manual activities combined.

Distribution of Unimanual Activities

In spite of the differences in percentages indicated in Table Ia, no significant age effect was observed on the distribution of UAs (F = 3.19; d.f. = 1, 14; n.s.); the same conclusion applies for sex (F = 1.55; d.f. = 1, 14; n.s.).

Table II shows the distribution of these activities for adults and young according to the position of objects manipulated.

TABLE II

Position of Objects for UAs: Percentages and Total Number for Each Subgroup

	In front	Ipsi.	Contra.	Total
Adults	44.7%	50.0%	5.3%	839
Young	47.0%	51.0%	2.0%	927

Table II shows that 94.7% of the reaches made by adults (and 98% made by the young) occurred when the object was positioned in front of the subject or when this object was located on the same side as the hand used; although cross-reaching (i.e. the use of the contralateral hand) was more frequent in adults (44 instances) than in young (19 instances) this difference was by no means significant (F = 1.77; d.f. = 1, 14; n.s.).

When the hand chosen in unimanual activities was considered, the group as a whole showed an almost similar number of right handed (N = 873) and left handed (N = 893) usages. For this measure neither sex (F = .01; d.f. = 1, 14; n.s.) nor age effects (F = 3.51; d.f. = 1, 14; n.s.) emerged.

Analyses of Bimanual Activities

As already indicated in the data in Table Ia, the young showed a greater number of bilateral activities (BB) than adults (F = 7.38; d.f. = 1,

TABLE III

(a) Mean Percentage of Behaviours for Each Level of Prehension as a Function of Age Subgroup.

	S.L.	D.L.	
Adults	42.8%	57.2%	100%
Young	54.3%	45.7%	100%

(b) Mean Percentage of Behaviours for Each Age Subgroup as a Function of the level of Prehension.

	Adults	Young	
S.L.	44.0%	56.0%	100%
D.L.	56.0%	44.0%	100%

14; $p < .05$); this suggests that young baboons displayed less activities involving hand differenciation than did adults. Here again, no sex differences between males and females could be seen ($F = .46$; d.f. = 1, 14; n.s.). The distribution of bimanual asymmetric activities (BA) were very similar in both age groups ($F = .02$; d.f. = 1, 14; n.s.). Nonetheless, interesting differences appeared between age subgroups in terms of level of prehension.

Tables IIIa and IIIb show the mean percentages of BAs activities for young and adults at either the "same" (SL) or at "different" (DL) levels of prehension.

Adults clearly performed more activities of different levels than activities of the same level ($F = 56.28$; d.f. = 1, 8; $p < .001$); in contrast, the young carried out more activities of the same level than activities of different levels ($F = 70.51$; d.f. = 1, 6; $p < .001$). When one compares adults and young for SL (cf. Table IIIb), one can note that the young displayed more SL on average than adults ($F = 7.42$; d.f. = 1, 14; $p < .05$), whereas the inverse is true for DL ($F = 6.90$; d.f. = 1, 14; $p < .05$).

Manual Preference

The computation of the index of manual preference (I) leads to the following picture for the group of 18 baboons (cf. Figure 1): seven subjects could qualify as left handers (among which 6 were young), the rest (11 subjects) could be rated as right handers. As already noted for the UAs, the distribution of right and left was almost equal; since the curve shown on Figure 1 is regular, it tends to reject the idea of a strict division between right and left biases. Actually, when one considers the confidence intervals reported for each subject in Figure 1, only five subject could be called true right handers and two subject true left handers.

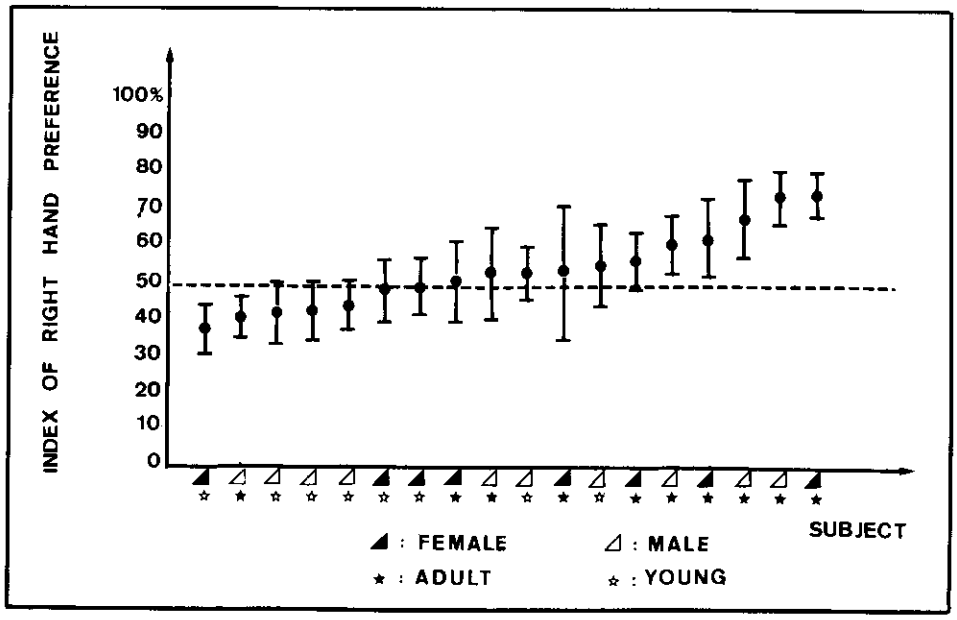

Fig. 1 — *Index of laterality. Percentages (with confidence interval) of right hand uses.*

We have already noted that the sex factor did not appear to have any effect on the use of hands. The same appears true in this case. No significant differences were found between males and females either in terms of preferential biases ($F = .02$; d.f. = 1, 14; n.s.), nor in terms of strength of laterality ($F = .13$; d.f. = 1, 14; n.s.).

Comparisons between adults and young give however a different picture, since adults had a significant right bias over young ($F = 9.85$; d.f. = 1, 14; $p < .05$). The strength of preference was also different (but only weakly significant according to usual statistical standards) between age subgroups, since adults tended to be more strongly lateralized than young ($F = 3.68$; d.f. = 1, 14; $p < .10$). Finally, we compared the preferential biases of the offspring (N = 8) with those of their mother. The Spearman rho obtained indicated a positive correlation (rs = .42), which was not significant at the 5% level.

DISCUSSION

After we have withdrawn the category "unknown" from the counting, we can observe that 75 percent of all manual actions are of an asymmetric nature (UAs + BAs). The following section will thus attempt to describe the content and form of these activities for the baboon.

The distribution of manual actions (cf. Table II) reveals that an average of 50.5 percent of them were realized with the ipsilateral arm: this indicates a clear tendency to use the forelimb nearer the object (as already observed by Cronholm et al., 1963, and Lehman, 1970, 1978b, 1980a). The choice of the hand is thus dependent on the relative position of the object. Moreover, the high percentage (45.8% on average) of activities "in front" of the object suggests that the baboons tend to position themselves so that they face the goal. Consequently, cross-reaching is rarely shown by the monkeys, although it is more frequent in adults than in young.

The distribution of the indexes of manual preference (Figure 1) doesn't show any clear bias toward the right or the left. Such data conform with the pattern described for related species (e.g., macaques, Warren, 1953; Kawai, 1967; Lehman, 1970, 1978a, 1980a), but also for chimpanzees (Finch, 1941) and non related species such as cats (Cole, 1955) and muridea (Papaouannou, 1972; Martin and Webster, 1974, Collins, 1975). Of course, given the variety of situations used here to measure laterality, our indexes are systematically weaker (a maximum of around 75 percent) than those obtained with a more limited number of tasks (cf. the literature on macaques mentioned above). The absence of a strong bias in the handedness of animal species is obviously in marked contrast with the strong right bias universally observed in humans (Hécaen and Ajuriaguerra, 1963; Oldfield, 1971). Possible exceptions from this rule are the case of gorillas which appear in most reports (Schaller, 1963; Fisher et al., 1982; Lockard, 1984) as being consistently right-handed, whereas rhesus macaques studied by Ettlinger and Moffet (1964) were found to show a significant left bias. Sex is not a significant variable in the determination of these indexes for baboons and this confirms previous studies (Lehman, 1978a, 1980b). The influence of a genetic component (maternal influence) in hand preference of young baboons has not been demonstrated: this result confirms the findings of Brooker et al. (1981), but is contrary to those obtained by Brinkman (1984) on crab-eating macaques.

The main effects seen in our study are related to the age variable. The first difference between adults and young concerns the total number of activities. The observation that young are more active than adults of both sexes has already been made when this same troop was tested for its reaction to novelty (Joubert and Vauclair, 1986). Besides the activity level, age is shown to have a significant effect on the frequencies of BBs/BAs, and SL/DL activities. Furthermore adults displayed a stronger preference than did young; this latter effect has also been reported in macaques (Lehman, 1978a 1980a; Brooker et al., 1981). This strength in preference is confirmed by the greater number of DL in adults than in young, thus implying that the former perform more asymmetric activities (see also the

differences for BBs where young subjects display more bilateral behaviours than adults).

From the preceeding considerations, it seems that lateralization is a process which develops during ontogeny. In addition to the factors related to handedness (bias and strength), the fact that adults show more differenciated activities (cf. the SL/DL distribution) with each hand, might suggest a different organization of bimanual collaboration compared to younger subjects. This can be further exemplified by the fact that adult baboons did perform more bimanual activities on a single object than did young. It can thus be of interest to relate handedness and bimanual collaboration (in the manner Bresson et al., 1977, have studied it in human infants) in primates and to look at their intertwining during ontogeny.

Abstract

Hand usage was studied in a troop of 18 Guinea baboons (10 adults and 8 young) for spontaneous activities. Handedness was determined by an analysis of unimanual activities and bimanual asymmetric activities. The distribution of preferential biases gave 5 right-handers and 2 left-handers, other subjects being ambidextrous. Main effects were age related: the strength of the preference was greater for adults than for young; moreover, bimanual activities performed by the adult group were more asymmetric than those realized by the subgroup of young. Laterality thus appears to develop during ontogeny in baboons.

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