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Handedness and Bimanual Coordination in the Lowland Gorilla

Joël Fagot, Jacques Vauclair
Laboratoire de Neurosciences Fonctionnelles, CNRS, Marseille, France

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Abstract. One could hypothesize from previous studies that gorillas, as a group, might show a right-hand preference, making this species an exception among nonhuman primates. A study of 10 captive gorillas observed while reaching for food and tested on unimanual and bimanual tasks does not support this conclusion. Instead, the present study found (a) a symmetrical distribution of subjects with right-hand (n = 3), left-hand (n = 3), and no hand preference (n = 4) when simply reaching for food and (b) a left-hand preference by 7 of 8 gorillas tested on a spatial task requiring precise alignment of two openings. These results stress the importance of considering the kind of task employed in the assessment of lateral preferences. Furthermore, it is suggested that it might be useful to distinguish between the handedness of a gorilla when simply reaching and its manual specialization for novel and complex tasks.

It is widely recognized that 9 out of 10 humans preferentially use their right hand to perform unimanual activities; this functional asymmetry is relatively stable in different populations [Salmaso and Longoni, 1985] and may constitute a characteristic of the human species. In contrast, roughly equal frequencies of right- and left-handers are generally found in studies of rats, cats and nonhuman primates [see for reviews, Walker, 1980; Warren, 1980]. The fact that individual animals manifest a hand preference but that there is not a consistent hand preference within nonhuman species as a whole makes it especially important to investigate this question in ape species, because of their phylogenetic closeness to man.

Anatomical differences between the cerebral hemispheres have been reported for apes [see for review, Witelson, 1977] and more recently for macaques [Falk et al., 1986]. For example, Groves and Humphrey [1973] in their examination of gorilla skulls have shown that only mountain gorillas had significant hemispheric differences in the distance from the anteriormost point of the temporal fossa to the gnathion. Another comparative study of the height of the posterior end of the sylvian fissure for each hemisphere found that the right sylvian point was higher than the left (by 3–5 mm) in 2 of 7 gorilla brains (the differences for the other brains did not exceed 3 mm), but more striking differences were measured for *Pongo* and *Pan* [LeMay and Geschwind, 1975].

From the few reports on hand preference in gorillas (see top section of table I), one could conclude that this ape sample is comparable to humans in the sense that 15 animals preferred the right hand, 1 the left hand and 2 animals were not showing any significant preference; moreover, this right preference is also reported for the hand initiating the chest beating [Schaller, 1963]. These results are intriguing in light of the absence of an apparent hand preference in chimpanzees [Finch, 1941; Marchant and Steklis, 1986]. However, because of the small sample size, the variety of tasks employed in different studies, and a lack of precise control over the placement of objects relative to the subject's hand, it is premature to conclude that gorillas show a hand preference comparable to humans.

The present study was conducted on the group of 10 gorillas of the Barcelona Zoo to experimentally test the hypothesis of right-hand dominance. In addi-

Table I. Summary of the main studies of hand asymmetry in gorilla species

Reference	Subjects[1]	Task	Results
Yerkes, 1927	mountain gorilla, 1 female	object manipulation	right-hander
Riess et al., 1949	lowland gorilla 1 male and 1 female	several activities	2 right-handers
Hass, 1958	lowland gorilla, 3 male juveniles	several activities	all right-handers
Schaller, 1963	mountain gorilla[1]	spontaneous feeding	'ambidextrous when the food was in front of them'
Fischer et al., 1982	lowland gorilla, 4 female adults	reaching	all right-handers (96% right usage for the group)
Lockard, 1984	lowland gorilla 2 male and 3 female adults 2 male and 1 female juvenile	spontaneous foraging	5 right-handers and 1 left-hander, 2 ambidextrous
Preilowski and Leder, 1984	lowland gorilla, 2 male and 3 female adults, 1 female juvenile	several kinds of reaching and object manipulation	'no interindividual consistency in the direction of preferences' (preferences are not given)
Schaller, 1963	mountain gorilla, 8 male adults	chest beating	59 out of 72 displays were performed with the right hand first
Dimond and Harries, 1984	lowland gorilla 2 male and 1 female adult 2 male and 3 female juveniles	face touching	4 left-handers, 4 with no preference (after recalculation of the original data [Suarez and Gallup, 1986]

[1] No indication is given when sex and or age were not provided in the original paper or are unknown to us.

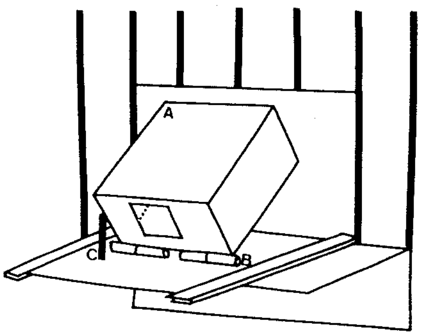

Fig. 1. Box apparatus used for tasks 2a and 2b. The stop screw was not part of the apparatus in task 2a, allowing the box to remain open once the gorilla lifted it. Addition of the stop screw in task 2b required the gorilla to keep the box lifted in order to retrieve the food reward. A = Metal box; B = hinge; C = stopscrew.

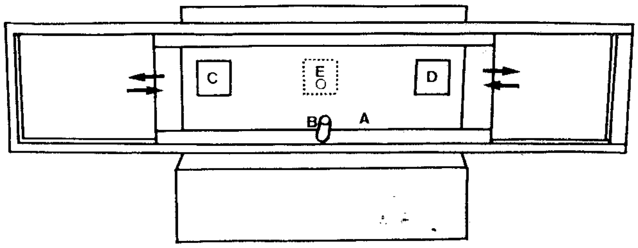

Fig. 2. Sliding panel apparatus used for task 3. The gorilla had to move the sliding panel (A) by the handle (B) and to adjust one of the windows (C or D) in front of the aperture (E) where the hazelnut was located.

tion, the study investigated the relationship between hand preference and bimanual coordination. The subjects were observed while reaching for food and during two experimental tasks, opening a box and sliding a panel, which involved performing an intermediate act to get access to a food item. These last two tasks could be solved either unimanually or with both hands.

Methods

Subjects

The 10 lowland gorillas *(Gorilla gorilla)* employed in this study were living in the Barcelona Zoo (Spain). The group was composed of 7 females (3 wild-born and 4 zoo-born) and 3 males (1 wild-born and 2 zoo-born) ranging in age from 5.3 to 25 years at the time of the study (October 15–30, 1986; see table II in results for further details). All subadults and juveniles were sired by COP ('Snowflake'), the famous white gorilla. Subjects lived by age groups in three different outdoor enclosures connected to inside cages where our tests were made.

Apparatus

Box Tasks. This apparatus consisted of a metal box (15 cm × 15 cm × 8 cm) mounted to a board by a hinge such that the whole box could rotate open so that the subject could obtain a hazelnut left on the horizontal board underneath the box (fig. 1). The box was attached outside the experimental cage at a height of 50 cm from the ground in front of a hole (25 cm × 20 cm). As originally constructed, the box remained raised once the gorilla lifted it (task 2a). In order to require the use of both hands, a stop screw was added near the back side of the box which caused the box to fall shut if the subject did not hold it open (task 2b).

Sliding Panel Task. This apparatus consisted of a transparent Plexiglas panel with two windows (5 cm × 5 cm). The panel could slide laterally in both directions in front of a 5 cm × 5 cm aperture made in a metal panel. The subject's task was to move the panel until one of the windows was in front of the central aperture allowing access to a hazelnut (fig. 2). If a window in the plexiglas panel was not precisely aligned with the aperture in the metal panel, the gorilla could not take the hazelnut. The apparatus was mounted outside of the experimental cage at a height of 50 cm from the ground. The subjects could manipulate the apparatus with one or two hands through a 40 cm × 20 cm hole. At the start of each trial, the goal window was positioned exactly between the two windows in the sliding panel.

Procedure

Task 1. The animals were observed for their unimanual hand preference when reaching for several food items (pieces of orange or banana or peanuts) thrown on the floor of the outside enclosures. Preliminary observations indicated that most consistent reaching occurred when the gorillas were standing quadripedally. Therefore we tabulated only reaching that occurred in that posture. Data were collected on the active hand (right or left) and on the position of the food before reaching (in front of the subject, in the contra- or ipsilateral hemifield to the hand used). Only reachings reflecting a real choice between hands (namely reaches performed when the food was in the midsagittal plane or acts of cross-reaching) were eventually used for analysis. A minimum of 100 such acts were collected per animal out of a total of 1,830 observations for the group as a whole.

Taks 2. For the box-opening task, we considered two situations: task 2a (30 trials per animal), where the box remained raised after opening, and task 2b (30 trials per animal), where the box had to be actively held up to obtain the hazelnut. For each trial in each situation, the strategy used by the subject was recorded following a coding system adapted from Ramsay and Weber [1986], namely the same hand raised the box and then removed the food (left/left, right/right), or one hand raised the box and then the other hand removed the food (left/right, right/left), and finally one hand raised the box, the other hand held the box and the leading hand removed the hazelnut (left-right/left, right-left/right). As can be seen from these possible strategies, the task could be performed with one or two hands.

Task 3. 30 trials per subject were run with the sliding panel task. For each trial, we recorded the hand which moved the Plexiglas panel and the hand that reached for the food. Here again, the task could be performed with one or two hands.

VIR and BIM did not adapt to the isolation necessary for the experiments and for these 2 subjects only results from task 1 are reported below. The other subjects learned both tasks very rapidly after the experimenter demonstrated raising the box and sliding the panel 10–15 times while randomly varying the hand used and the direction of the movements. For practical reasons, task 3 was presented first, followed by task 2a and then task 2b, whereas the reachings (task 1) were recorded throughout the 2 weeks of experimentation.

The three tasks we employed can be ranked in terms of the number of steps, and their precision, required to get the food. Thus, task 1 only required a simple reaching movement toward the food item; task 2 required one or two gross intermediate actions (i.e. raising the box or raising and holding the box) before attaining the food, whereas task 3 imposed an initial action consisting of a lateral displacement of the panel followed by a precise alignment of the window and aperture to allow access to the food. In this third task, any misalignment of the two openings prevented the gorilla from obtaining the hazelnut.

Table II. Name, sex, age, number of left- and right-hand usages for task 1 and statistical conclusion regarding manual preference for each gorilla

Name	Sex origin	Age years	Left hand	Right hand	χ^2	p value	Bias
YUM	F, W	25	23	83	33.4	<0.001	RIGHT
NDE	F, W	23	78	33	18.2	<0.001	LEFT
BIM	F, W	21	51	56	0.2	n.s.	NP
MAC	F, Z	8.8	82	23	32.2	<0.001	LEFT
NTA	F, Z	7.9	87	29	29.0	<0.001	LEFT
VIR	F, Z	7.8	37	75	12.9	<0.001	RIGHT
KEN	F, Z	5.3	47	83	10.0	<0.01	RIGHT
COP	M, W	24	75	71	0.1	n.s.	NP
URK	M, Z	8.8	49	67	2.8	n.s	NP
BIN	M, Z	5.3	75	79	0.1	n.s.	NP
Total (n = 1,203)			604	599			

M = Male; F = female; W = wild-born; Z = zoo-born; NP = no preference; n.s. = nonsignificant.

Table III. Number of unimanual solutions per subject for the 3 tasks, bias and corresponding percentages of hand preference

Subject	Task 1			Task 2a			Task 2b			Task 3		
	P	%		P	%	n	P	%	n	P	%	n
YUM	R	78				1			0	L	100	30
NDE	L	70		L	97	30	L	90	30	L	100	30
MAC	L	78				0			1	L	100	17
NTA	L	75				3			0	L	100	29
KEN	R	64		R	100	15			0	R	89	28
COP	NP	51	(L)	R	72	25	NP		9	L	97	30
URK	NP	58	(R)			3			0	L	100	30
BIN	NP	51	(R)	L	90	29			3	L	96	26

Preferences (P) are indicated by an L (left), R (right) or NP (no preference). n = Number of unimanual solutions out of 30 trials. The statistical significance was computed with a χ^2 test ($p < 0.05$) when $n \geq 10$ or by binomial test ($p < 0.05$) if $5 < n < 10$.

Results

Unimanual Reaching

Of the 1,830 food reachings, 34.3% (n = 627) were made with the hand nearest to the food, 60.9% (n = 1,115) were made in the midsagittal plane and 4.8% (n = 88) involved the use of the contralateral hand (cross-reaching). Because these last two categories reflect a true choice of hand we used only these events (n = 1,203) for statistical analysis (table II).

3 gorillas (YUM, VIR, KEN) showed significant right-hand preference, 3 others (NDE, MAC, NTA) were left-handers, and 4 others showed no significant hand preference (BIM, COP, URK, BIN; table II): For the group as a whole, the use of the left or right hand was almost equally distributed (599 right vs. 604 left).

No significant correlation (r = 0.07, n.s.) was found between the age of the subjects and the strength of the preference (deviation from 50%). In addition, the distribution of hand preferences was comparable among age subgroups: 1 right-hander and 1 left-hander in adults, 2 left-handers and 2 right-handers among juveniles. Finally, the subjects which showed a significant hand preference did not cross-reach more often than subjects which showed no hand preference (Mann-Whitney U test, U = 13, n.s.).

Unimanual Strategies for Tasks 2 and 3

Table III summarizes the one-handed strategies for the three tasks: 4 of 8 subjects regularly solved task 2a with a single hand while the other 4 routinely used both hands. The group as a whole solved this task unimanually 44% of the time. Unimanual solutions were rarely seen in solving task 2b (18% on average for the group). This percentage was essentially due to 1 subject (NDE) who used a single hand very frequently; in her case the same hand (the left) sneaked under the box, raised it a bit and grabbed the food. All subjects used a single-handed strategy to solve the sliding panel task (task 3) and employed it on 92% of the trials.

The frequency of unimanual solutions for the three tasks was not significantly related to the age of the animals (r = 0.43, n.s.). In addition, subjects presenting a significant hand preference during the simple reaching of task 1 did not show more one-handed strategies (47%) than subjects showing no hand preference on task 1 (57%; Mann-Whitney U test, U = 11, n.s.).

3 of the 4 subjects regularly employing one-handed solutions for tasks 2a and 3 showed consistent hand preference across the tasks. 1 subject (COP) showed no consistency in hand preference across tasks.

Comparison of hand preference in simple reaching (task 1) with the preferences observed for tasks 2 or 3 indicated that the same hand was used for both tasks by 4 of the 5 gorillas displaying a preference on task 1. Moreover, 7 of 8 subjects used their left hand when they solved task 3 unimanually.

Bimanual Strategies for Tasks 2 and 3

For the purpose of the analysis, we have distinguished the hand used to move the apparatus ('move') from the food prehension itself ('take'). Table IV re-

Table IV. Number of bimanual solutions per subject for tasks 2a, 2b and 3, corresponding bias and frequencies

Subject	Move (box or panel)						Take					
	task 2a		task 2b		task 3		task 2a		task 2b		task 3	
	P	%	P	%	P	%	P	%	P	%	P	%
YUM	L	97	L	100			L	86	L	100		
NDE												
MAC	L	96	L	97	L	92	R	96	R	100	R	92
NTA	R	100	R	93			L	100	L	97		
KEN	L	90	L	100			NP		R	83		
COP			R	90					L	90		
URK	NP		R	73			R	81	NP			
BIN			L	89					R	89		

Preferences (P) are indicated by an L (left), R (right) or NP (no preference) for each action. YUM used the left hand to raise the box, the right hand to hold it open and then used the left hand to take the food.

ports the individual gorilla's hand preferences during such bimanual strategies.

When one considers the preferences for the apparatus manipulation (move) independently from the reaching itself (take), table IV reveals that the 4 gorillas (YUM, MAC, NTA, KEN) which showed significant moving preferences in at least two out of three tasks used the same hand. The 3 gorillas (YUM, MAC, NTA) which showed a significant taking preference for at least two out of the three tasks consistently used the same hand. In no case did a subject show a different preference across tasks 2 and 3. However, not all the subjects used the hand preferred for task 1 in the same manner during bimanual activities. For example, MAC and NTA were both left-handers in task 1 and used their right hand either to move (NTA) or to take (MAC) in tasks 2 and 3.

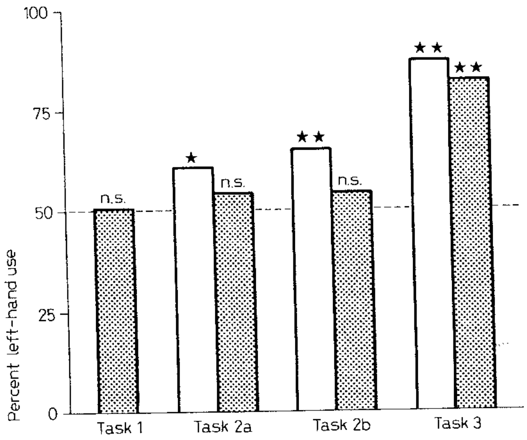

Fig. 3. Percentage of left-hand use for moving (□) or taking (▤) an object across four tasks for 8 gorillas. * $p < 0.01$; ** $p < 0.001$; n.s. = nonsignificant.

Overall Comparison of Hand Use across Tasks

It is already apparent from the data reported in table III that the gorillas tended to use the left hand more frequently than the right hand when they solved task 3 unimanually. In order to further analyze this trend, all right or left for move acts and all right or left for take acts for a particular task were summed for the 8 subjects, and the percentages were compared to the 50% chance level using a test for the significance of a proportion [Bruning and Kintz, 1977]. The average percentage of left-hand use as a function of the type of task is represented in figure 3. It can be seen in that figure that a significant preference for the left hand appeared in the execution of the moving actions in tasks 2a, 2b and 3 (60.4, 65 and 87.1%, respectively). For the taking action, such a left preference appeared only in task 3 (82.1%) and not in tasks 2a and 2b (54.2% for each task).

Discussion

The present results demonstrate the following four points.

(1) As shown in tables III and IV, most gorillas have expressed a significant hand preference in the experimental situations. Interestingly, the preferences observed in task 3 were markedly stronger than those seen in the simple reachings. For example for NTA, the left hand was used to perform 75% of the simple reachings and 100% of the adjustments of the Plexiglas panel of task 3. Moreover, all gorillas but 1 (KEN) have expressed a significant left-hand preference to solve task 3 (table III); such a bias for the group was not observed in task 1 in which a left-hand preference was noted for NDE, MAC and NTA, a right-hand preference for YUM and KEN and no significant preference for COP, URK and BIN. It thus appears that the strength, the direction and consequently the shape of the distribution of the preferential biases for the group could be influenced by the kind of task employed.

(2) In a recent review about primate handedness, MacNeilage et al. [1987] propose to reinterpret manual preferences as follows: (a) a left-hand preference at the population level for visually guided activities such as the simple reaching for food, and (b) a right-hand preference at the population level for the most 'demanding manipulative act'. In short, their theory predicts that, whatever the bias, hand preferences should be distributed asymmetrically in the populations. Such a distribution has been observed for the sliding planel task but not for the pure reaching task, which led to a symmetrical distribution of the two biases. In addition, the manipulatory task of the box opening has not provided the preferences which could be expected from this theory, since we found a left-hand preference for opening and no trend for reaching in the box. A different analysis applied by Young et al. [1983] to human laterality seems to be relevant to describe our results. These authors have proposed a distinction between two kinds of manual preference: 'handedness' and 'manual specialization'. According to these authors, handedness is characterized by a consistent hand usage on simple, highly practised tasks. In contrast, manual specialization is characterized by lateral preferences on novel, complex (e.g. bimanual) tasks. These authors also suggested that manual specialization more directly reflects hemispheric specialization than the preferences expressed in simple handedness.

During the simple reaching task, we obtained a symmetrical distribution of right-handers (n = 3), left-handers (n = 3) and subjects showing no preference (n = 4). One can hypothesize that this kind of distribution corresponds to what Young et al. [1983] call handedness. However, a clear hand preference for the group appeared in bimanual tasks, for the moving action in tasks 2a, 2b and 3 and for the taking action in the sliding panel task. Such a left-hand preference which appeared in solving novel and relatively complex tasks could reflect manual specialization in the sense of Young et al. [1983]. In other words, preferences seen in simple reaching tasks might represent only one aspect of laterality. It is interesting to note that most studies which investigated gorilla handedness used reaching and simple object manipulation (cf. table I).

(3) In a previous study [Vauclair and Fagot, 1987], we demonstrated an effect of age on the strength of manual preferences of Guinea baboons. Such differences between age subgroups were not observed in the present study, presumably because manual preferences were already well established in the gorilla group, as the youngest subject was more than 5 years old at the time of the testing.

(4) As already stated, a left-hand preference for the group as a whole appeared in tasks 2a, 2b and 3 for the moving action and also in task 3 for the taking action (fig. 3). The taking action in tasks 1, 2a and 2b does not differ in the sense that they consist of reaching movements on a flat surface. However, in task 3, this taking action involves the extraction of the food item from a small hole. The group presented the same left-hand preference for the moving action for tasks 2a, 2b and 3. Since task 3 was presented first (before 2a and 2b), one can rule out a training effect to account for this left-hand preference. One can hypothesize that the left-hand preference observed is dependent upon the characteristics of the tasks, most probably their spatial requirements. The finding of a left-hand preference on tasks 2a, 2b and 3 is similar to the demonstrated right hemisphere specialization (left-hand advantage) for humans solving visuospatial tasks [Nachson and Carmon, 1975; Ledoux et al., 1977].

Although the present work must be considered as preliminary due to the small sample size, our results contradict the idea of a right-hand preference in gorillas. The phenomenon of a left-hand preference observed should be looked for in this and other primate species performing tasks similar to those employed here.

Acknowledgments

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Joël Fagot
Laboratoire de Neurosciences Fonctionnelles
31, Chemin Joseph Aiguier
F-13402 Marseille Cedex 9 (France)