

HANDEDNESS AND MANUAL SPECIALIZATION IN THE BABOON

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Abstract—Manual preferences of six baboons were tested with three kinds of experimental tasks: (1) a simple reaching on a board or in a hole; (2) a box opening; (3) two visuo-spatial tasks requiring precise alignments of apertures. The distribution of right and left hand preferences was found to be symmetrical for the simple reachings (3 right- and 3 left-handers) and was consistent with the preferences in the box opening task. However, manual tasks with strong visuo-spatial components gave a unimodal distribution with a left hand preference for the group for aligning and adjusting the apertures. These results suggest the coexistence within an individual of two types of preferences according to the distinction between handedness and manual specialization.

INTRODUCTION

THE EXISTENCE of functional asymmetries in humans is now well established [1]. However, it is unresolved whether there are analogous asymmetries in animals. Nonhuman primates are obvious candidates for the study of laterality in animals because of their relatedness to man. Although some nonconclusive results have been reported [15, 27] there is increasing evidence that apes and monkeys present several kinds of anatomical and/or functional lateral specialization: for anatomical differences [2, 9, 12, 24, 36]; for functional differences [3, 5, 11, 14, 16, 17, 18, 19, 28].

In contrast, there is little evidence of manual preferences across a population of nonhuman primates. Generally, the distribution of manual preferences in a population is described as U shaped with an equal number of left- and right-handers [22, 23, 32]. In addition those preferences are considered to be situation and task specific. For example, hand preference in a reaching task was found to be dependent on the testing situation (e.g. a primate chair or a WGTA; [4]), on the position of the food relative to the animal [22] and on the age of the animal [22, 23]. Effects of unilateral ablations of associative cortex on a visual discrimination task were independent of the preferences as determined by a reaching task [33]. From these results, WARREN [34] concluded that handedness in animals is primarily the result of experience and that lateral differences are probably more analogous than homologous to those observed in humans [35].

However, some studies contradict this common view of primate handedness since they suggest an asymmetrical distribution of the left and right preferences. For example, KAWAI [20] found a unimodal asymmetrical distribution of the preferences in a one-handed catching behaviour in *Macaca fuscata*. With a simple reaching task, SANFORD *et al.* [29, 30] reported more of left- than right-handers in 25 *Galago senegalensis* tested in an erect posture, but the

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distribution became bimodal when the animals were tested in an horizontal stance [29]. The studies of ETTLINGER *et al.* have demonstrated a left hand preference during initial trials in visual discrimination tasks involving hand use [6, 7, 10]. The replication of the same kind of tests performed in the dark (haptic discrimination) has suggested an advantage either for the left [26] or for the right hand [7]. Given those results, MACNEILAGE *et al.* [25], in contrast to WARREN [35], concluded that there is: (1) a left hand specialization (right hemisphere) for visually guided movements, such as reaching for food; (2) a right hand specialization for manipulation and for bimanual coordinated movements.

In a previous study of 8 *Gorilla gorilla* [8], we found the very intriguing result that the distribution of manual biases was symmetrical in a simple reaching-for-food task, whereas 7 of 8 gorillas preferentially used their left hand in a visuo-spatial task requiring them to precisely align two openings. A theoretical framework provided by YOUNG *et al.* [37] was used in the discussion of our work on gorillas to account for the two types of manual distribution we observed. YOUNG *et al.* have distinguished between the concept of handedness which is more readily expressed in simple and familiar activities and the concept of manual specialization which applies to novel and relatively complex tasks. The present work extends our previous work in the gorilla to an Old World monkey species. We thus tested six Guinea baboons during a simple reaching for food task, a box opening task and a visuo-spatial task similar to those used with the gorillas. In addition, a novel apparatus (cf. VSPT, see below) was introduced in order to constrain the simultaneous use of both hands. Special attention was given to the manual preferences expressed in each situation and to the related bimanual coordinations.

EXPERIMENT I

Methods

Subjects. The subjects were six male Guinea baboons (*Papio papio*), neurologically and sensorially intact. Five of them (wild-born) were about 8 years old, the other (captive-born) was 4 years old at the time of the testing. Their manual preferences had been assessed two years before the present investigation through observation of their spontaneous hand use [31]. Three baboons (GRE, MAC, YEL) had shown a right hand preference and the others were classified as ambidextrous since they expressed a nonsignificant preference for the left hand (RUM and BIA) or for the right hand (POM). The baboons lived in a social group of 28 baboons in an outdoor enclosure (about 640 m²) connected by a tunnel to a 4 m × 3 m monkey house. The six subjects used for the study were the only group members which accepted being isolated for the testing periods.

Apparatus. An experimental cage (50 cm × 50 cm × 80 cm) was attached to a 40 cm × 35 cm opening in the fence inside the housing area. The sides of the cage were adjustable so that the width was 35 cm for the older baboons and 28 cm for RUM, the younger. At one end of the cage, different kinds of manipulanda could be attached by vertical slides. Two large symmetrical openings and a face mask with two eye-holes permitted free manipulation with one or both hands in full view of the subject.

Board task. This apparatus consisted of a horizontal metal board (40 × 20 cm; cf. Fig. 1) presented at various distances from the animal and at various heights from the floor (see section on Procedure below). In each trial, a hazelnut was placed on a mark in the centre of the board.

Box task (BT and BST). A metal box (15 cm × 15 cm × 8 cm) was mounted to a board (40 cm × 20 cm) by a hinge such that the whole box could rotate open. By lifting the whole box, the subject could obtain a hazelnut left on the horizontal board underneath it (cf. Fig. 1). The box was positioned in such a way that its centre was at 35 cm in front of the animal, 5 cm under the level of its eyes. As originally constructed, the box remained raised once the baboon lifted it (BT). In order to require the use of the two hands (BST), 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. This task was the same as described in FAGOT and VAUCLAIR [8].

Horizontal sliding panel task (HSPT). This apparatus consisted of a transparent Plexiglass window (46 cm × 20 cm) with two symmetrical lateral windows (5 cm × 5 cm) each at 10 cm from the center (cf. Fig. 1). The panel could slide laterally in both directions in front of a vertical metal board with a central (5 cm × 5 cm) aperture. A metal handle (6 cm long and 1.5 cm dia) permitted movement of the Plexiglass until one of the two windows (the left or the right) was positioned in front of the central aperture allowing access to a hazelnut. For that action, the panel had to be moved at least 15 cm. If the sliding window was not precisely aligned with the central aperture, the

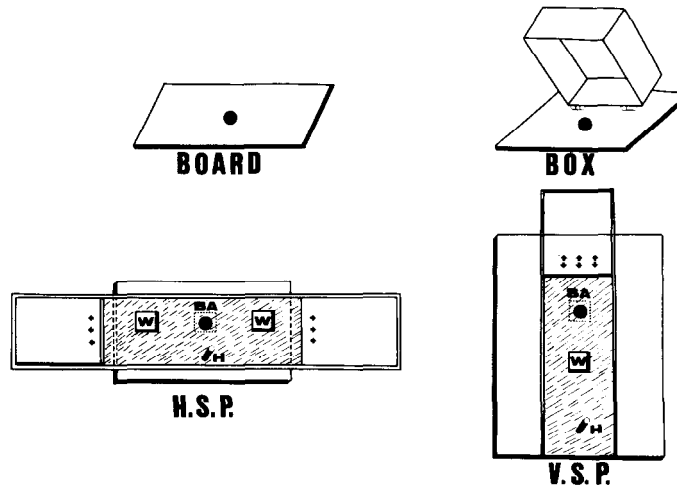


FIG. 1. The apparatus used in the board task, in the two box tasks (BT and BST) and in the two sliding panel tasks (HSPT and VSPT). BA, board aperture; W, Plexiglass window; H, handle; black dot, incentive. The hatched surface shows the sliding panel. The arrows indicate the direction of the panel's movements.

subject could not easily grasp the hazelnut. This apparatus was located 35 cm in front of the animal and 5 cm below eye-level and it could be manipulated either uni- or bimanually. At the start of each trial, the goal window was situated exactly between the two lateral windows in the sliding panel. This task was the same as described in FAGOT and VAUCLAIR [8].

Vertical sliding panel task (VSPT). This manipulandum consisted of a vertical transparent sliding panel (33 cm \times 15 cm) with only one window (5 cm \times 5 cm; cf. Fig. 1). This panel could slide vertically in both directions in front of a metal board with a central (5 cm \times 5 cm) aperture. A metal handle (8 cm in length and 2.5 cm dia) permitted lifting and adjusting the moving window on the panel in front of the central aperture, in order to get the hazelnut. If the subject failed to keep the Plexiglass panel raised, it would fall down. The two windows were correctly aligned when the panel was lifted 15 cm. The goal window was 35 cm in front of the animal and 5 cm below eye-level. As it was impossible to adjust the panel and to simultaneously take the hazelnut with the same hand, this apparatus forced the baboons to use both hands to solve the task.

Procedure

During the experiments, each subject was isolated in the housing area. The experimental cage being left open, the baboon voluntarily entered the cage and positioned itself in front of the apparatus. The board task was presented first, followed by the box task without the stop-screw, the box task with the stop-screw and then by the horizontal and vertical sliding panel tasks. However, for two subjects (POM and RUM), the vertical panel was presented before the horizontal one (when presented with HSPT first, both subjects expressed no interest). One month after the test trials, each subject received 100 retest trials for the board task and 50 retest trials for the remaining tasks. For retests, tasks were presented in an inverse order.

Board task. In order to determine hand preference in a simple reaching task and to determine the dependence of the preferences from the location of the food relative to the animal, the board was presented in four positions which corresponded to two distances from the baboon (20 or 40 cm) and to two heights from the floor (25 or 50 cm). Each subject received 50 scored trials in each situation (one situation/day during 4 days) selected by a balanced plan. In all situations, the hazelnut was left in the midsagittal plane of the animal.

Box task. For this task, a hazelnut was hidden under the closed box and two situations were considered. The first one (BT; 100 scored trials/animal, 25 trials/day in 4 days) consisted of opening the box when the lid remained raised without being held. The second situation (BST; 100 scored trials per subject, 25 trials/day in 4 days) consisted of opening the box when the lid had to be actively held in order to obtain the hazelnut.

Sliding panel tasks. A hundred scored trials per subject (25 trials per day during 4 days) were run with each sliding panel task. Given the relative difficulty of the horizontal task for the baboons, the experimenter demonstrated the sliding of the panel while randomly varying the hand used and the direction of movement. An average of 11.3 demonstrations ($SD=9.97$) were necessary until the baboons could do the task. The vertical task did not require demonstration.

Coding. The reachings on the board were coded according to the hand used (left or right). For the other tasks, we recorded the strategy used as follows: L/L or R/R when the same hand (left or right) was used for raising the box (or

moving the panel) and taking the food; L/R, R/L, B/R or B/L, when one (left or right) or both hands were used for raising the box (or moving the panel) and the other hand (left or right) was used for taking the food; L-R/L or R-L/R, when one hand raised the box (or moved the panel) and the other hand kept the box open (or adjusted the panel), while the first hand removed the food.

Statistical design. Computation of individual preferences were realized with a Chi square test (left vs. right hand uses, $P < 0.05$) or Binomial two-tailed test ($P < 0.05$) if $5 = < n = < 10$. Binomial two-tailed tests were also used to establish the significance of the group's preferences. Spearman rank correlation coefficients were employed to study test-retest reliability. In order to study interactions between hand preferences in the board task and choices in other situations, ANOVAs were performed. The general design was: hand preferences on the board (left or right) \times Session (of 25 trials); subject was the random factor. The dependent variable was the number of left (or right) hand uses in a given task.

Results

Manual preferences in the board task. When the hazelnut was left on the board, all baboons used a one-handed strategy to pick it up and to bring it to their mouth. The preferences were exactly the same for the four positions of the board, since all subjects used the same hand in the same proportion for all positions (except BIA which inverted its preference in only 3 cases out of 200). Thus, all 200 trials per subject were pooled for the determination of manual preferences. Manual preferences and the corresponding percentages of left hand usage are summarized in Table 1. Three subjects (MAC, GRE and POM) were found exclusive right users whereas the three others (YEL, BIA, and RUM) showed a significant left hand preference in the board task.

Table 1. Percentages of left hand use for reaching on the board (all locations pooled) and hand preferences for six male baboons

Subject	MAC	GRE	POM	YEL	BIA	RUM
Left use	0%	0%	0%	100%	99%	100%
Hand pref.(*)	Right	Right	Right	Left	Left	Left

(*) Manual preferences were determined by a Chi square (right vs left hand use; $P < 0.05$).

Manual preference during box and sliding panel tasks. For the two box tasks as well as for the sliding panel tasks, we distinguished the hand which opened the box or moved the panel from the hand which took the food. In addition, for VSPT the hand used to do the final adjustment of the window was also recorded. Hand preferences expressed for each task when they were solved unimanually are summarized in Table 2 (VSPT was never solved unimanually). Table 3 provides the hand preferences when the tasks were solved bimanually.

Table 2. Hand bias, frequencies and number of unimanual solutions per subject for the board, the box (BT and BST) and the horizontal sliding panel task (HSPT)

Subject	Board	BT	BST	HSPT
MAC	R 100 (200)			L 67 (48)
GRE	R 100 (200)	R 100 (10)		L 95 (41)
POM	R 100 (200)			L 88 (33)
YEL	L 100 (200)			R 90 (60)
BIA	L 99 (200)	L 100 (8)		L 100 (35)
RUM	L 100 (200)		L 100 (6)	L 100 (93)

The numbers of unimanual solutions indicated in parentheses. Biases were determined by a Chi square (right vs left hand uses, $P < 0.05$) or a Binomial two-tailed test if $5 = < n = < 10$. L, left; R, right; N.P., no preference.

Table 3. Hand bias, and corresponding frequencies per subject for the bimanual solutions in each task. (cf. legend of Table 2.) *in these cases a left bias appears with $P=0.055$

Subject	Move		Adjust			Take			
	BT	BST	HSPT	VSPT	VSPT	BT	BST	HSPT	VSPT
MAC	R 100	R 99	L 87	L 75	L 91	L 100	L 98	R 86	R 91
GRE	N.P.	R 100	L 97	N.P. (*)	L 85	N.P.	L 100	R 97	R 86
POM	R 100	R 95	L 97	N.P. (*)	L 92	L 100	L 95	R 97	R 94
YEL	L 100	L 100	R 73	L 89	[L 98]	R 100	R 98	L 73	R 98
BIA	L 98	L 99	L 100	L 96	L 100	R 98	R 99	R 100	R 100
RUM	L 100	L 99	L 100	L 99	L 100	R 100	R 99	R 100	R 100

Box tasks (BT and BST). L/R and R/L were the most frequently observed solutions (97 on average out of 100 trials for BT and 98.5 for BST). B/L and B/R strategies were never seen for these two tasks; only two instances of L-R/L and one instance of R-L/R solutions were recorded. Unimanual solutions (L/L and R/R) were rarely used (6 on average for BT and 1 for BST). The only subject which partially solved the BST unimanually (RUM; 6 times out of 100) threw the lid up and grabbed the nut before the lid dropped. As indicated in Table 3, two subjects for the BT (MAC and POM) and three for the BST (MAC, GRE, POM) showed a significant right hand preference for the moving action. The others were consistent left hand users for the moving action in the two box tasks. Moreover, the hand preferentially used to lift the lid was strongly related to the manual preferences expressed in the board task [ANOVA: $F(1-4)=217$, $P<0.001$] in the sense that the hand which took the hazelnut during the board task was the hand used to open the box.

The taking action was generally performed with the hand other than that which opened the box. Table 3 indicates three right and two left takers for the BT and three right and three left takers for the BST.

Horizontal sliding panel task. B/R, B/L, L-R/L and R-L/R solutions were never recorded for that task. On average for the group, 51.7 trials (out of 100) were solved unimanually (L/L or R/R) and 48.3 were solved bimanually (R/L and L/R). When unimanual solutions were employed (see Table 2), five out of six baboons (MAC, GRE, BIA, POM, RUM) used their left hand significantly more often than their right. YEL, the sixth, preferred the right hand for that action. Similarly, when bimanual solutions were used, all the baboons (except YEL) showed a left hand preference for sliding the panel and a right hand preference for reaching for the food in the aperture. The inverse was true for YEL. Interestingly, the numbers of left hand movements and left hand takings were independent of the preferences for the board task [ANOVA for moving: $F(1-4)=0.34$, n.s.; ANOVA for taking: $F(1-4)=0.78$, n.s.].

Vertical sliding panel task. The six baboons used L/R or R/L solutions more often (77.3 on average out of 100 trials) than L-R/L or R-L/R (16.2) and B/R and B/L solutions (6.5). The analysis of variance revealed that baboons which had a right hand preference on the board employed less L/R or R/L solutions (62 on average out of 100 trials) than others (99.3) which had a left hand preference on the board [ANOVA: $F(1-4)=9.63$, $P=0.026$].

Four of six baboons (MAC, YEL, BIA, RUM) could be classified as left lifters of the vertical panel (see Table 3). GRE and POM showed a left hand preference for that action which was very close to statistical significance ($P=0.055$ each). If we consider those two last subjects as left lifters, we can then admit a left hand preference for the group as a whole (Binomial two-tailed test, $P=0.032$). Although all the subjects have shown a left hand preference to lift the panel, subjects which were classified as right-handers in the board task

used their left hand less often (66.5 on average out of 100 trials) than those which were classified as left-handers [94.6 on average; ANOVA: $F(1-4) = 28.6$, $P = 0.006$].

Table 3 shows a left hand preference for the six baboons for adjusting the Plexiglass window (Binomial two-tailed test, $P = 0.032$). Baboons which showed a left hand preference on the board task used the left hand for adjusting the window more often (on average 99 out of 100 trials) than those which showed a right hand preference [89 on average; ANOVA: $F(1-4) = 20.96$, $P < 0.01$].

All subjects expressed a right hand preference to take the hazelnut in the VSPT (Binomial two-tailed test, $P = 0.032$), since the left hand was used preferentially to perform the adjustment.

Test-retest reliability. Test-retest reliability was evaluated by a Spearman rank correlation coefficient comparing initial tests and post measurements. Table 4 gives the test-retest correlations for each task and action. All the test-retest correlations were positive. Moreover, except for HSPT, the correlations were significant which demonstrated a good stability of the preferences between both testing periods.

Table 4. Test-retest Spearman rank correlation coefficients and level of significance for each task and action; * = $P < 0.05$

	Board	BT	BST	HSPT	VSPT
Move	—	0.84*	0.86*	0.73	0.89*
Adjust	—	—	—	—	0.84*
Take	0.86*	0.83*	0.91*	0.52	0.94*

Discussion

To summarize, we obtained markedly different results between the board and box tasks and those obtained with the sliding panel tasks. The first two tasks produced an equal number of left- and right-handers. Moreover, bimanual solutions in the box tasks were strongly related to the preferences expressed on the board task. In contrast, for the sliding panel tasks, the group as a whole showed: (1) a left hand preference for the moving action (significant for the VSPT and a tendency only for HSPT); (2) a left hand preference for adjusting the window for the VSPT; (3) a right hand preference for the taking action in the VSPT.

One can hypothesize that these left hand preferences for the group correspond to a functional advantage in visuo-spatial tasks so that the left hand adjusted the panel which induced a right hand preference for the taking action. However, principally for VSPT, one can also hypothesize a right hand advantage in taking the incentive from the hole which required using the left hand to lift the panel (remember that all subjects had expressed a significant right hand preference for taking in VSPT). These two hypotheses were tested by two additional tasks.

EXPERIMENT II

Methods

Apparatus. Hole task (HT). This apparatus consisted of a vertical metal board with a hole (5×5 cm) in its center. The hole was adjusted at 35 cm in front of the animal and at 5 cm under the level of its eyes. On each trial, a hazelnut was left in the aperture.

Delayed vertical sliding panel task (DVSPT). This apparatus consisted of a vertical transparent sliding panel (33×15 cm) with a circular hole (2 cm dia) and a handle (6 cm long and 1.5 cm dia) located in a central position at 10 cm below the hole. The panel could slide vertically in front of a metal board with a median circular aperture (2 cm dia, initially positioned at 15 cm above the sliding hole) where a hazelnut was left; the panel fell down if the subject did not keep it raised. The board aperture was initially adjusted at 35 cm in front of the animal and at 5 cm below eye-level. When the panel was lifted up so that the sliding hole was exactly in front of the board aperture, the incentive fell down through the hole. A second Plexiglass prevented a direct access to the hazelnut during its fall so that the incentive fell into a pipe and was automatically delivered in the midsagittal axis of the floor of the cage. As the reinforcement was delayed and delivered in the cage, the adjustment action could be considered as relatively independent of the taking action.

Procedure. The same six baboons were used for these tasks. One month elapsed between the completion of the first experiment and the beginning of the second. For HT, each subject had to retrieve 100 hazelnuts in four sessions of 25 trials. The hand used (left or right) to take the incentive was recorded in each trial. For DVSPT, 100 trials were run per subject (25 trials per day during 4 days). For each trial, the hand(s) used to lift the panel (left, right or both) and to adjust it (left, right or both) were recorded.

Results

The manual preferences expressed for HT, for the moving and for the adjusting action of DVSPT, are summarized in Table 5.

Table 5. Manual preference and corresponding frequencies for HT and DVSPT (c.f. legend of Table 2)

	MAC	GRE	POM	YEL	BIA	RUM
HT	R 96	R100	R100	L 96	L 70	L100
DVSPT Move	N.P.	R 86	L 63	L100	L100	L100
DVSPT Adjust	L 63	R 91	L 84	L 98	L100	L 99

Manual preferences in the hole task. Table 5 shows three right- and three left-handers for that task. Moreover, these preferences are the same as those expressed in the board task (cf. Table 2).

Manual preferences in the delayed vertical sliding panel task. On average for the group, 3.8 (out of 100 trials) of the solutions employed to move the panel were bimanual. Table 5 shows a significant left hand preference to move the sliding panel for four subjects (BIA, RUM, YEL and POM) and a right hand preference for GRE (MAC showing no preference). Furthermore, ANOVA reveals that the baboons which had shown a right hand preference on the board task used their left hand to move the panel in DVSPT less frequently than those which had expressed a left hand preference [$F(1-4) = 17.8$, $P = 0.013$].

On average for the group, 12.8 (out of 100 trials) of the strategies employed to adjust the sliding hole were bimanual. Table 5 shows a left hand preference to adjust the panel for five subjects and a right hand choice for one subject (Binomial two-tailed test, $P = 0.22$, n.s.). The three left takers during the hole task (YEL, BIA and RUM) displayed the same hand preference for adjusting the panel. Among the three right takers during the hole task, two (MAC and POM) changed their hand preference in the adjustment and used the left hand. The other (GRE) was classified as a right adjuster.

GENERAL DISCUSSION

The board and the hole tasks produced a symmetrical distribution of right- and left-handers. Moreover, the preferences to solve the box task were closely related to the preferences on the board as well as in the hole. Thus, a strong inter-task coherence emerged

from this set of tasks. For the sliding panel tasks, the distribution of the two biases became unimodal both for the moving and for the taking actions (HSPT, VSPT). Although we cannot rule out some generalization from VSPT to DVSPT, the results of Experiment II (5 left adjusters) suggest that the strategies employed in the sliding panel tasks probably correspond to a functional advantage of the left hand in adjusting the panel. The two separate sets of manual biases obtained on the one hand with the board, the box and the hole tasks and, on the other hand, with the sliding panel tasks might suggest the intra-individual coexistence of two types of preference. A similar coexistence was also described for prosimians [29] and for apes [8].

The present data only partially agree with MACNEILAGE *et al.*'s [25] theory since we found a left hand preference for tasks with a clear visuo-spatial component. However, the bimodal distribution obtained with the board and the box tasks is not predicted by MacNeilage *et al.*'s theory. YOUNG *et al.* [37] have proposed for humans a model which may account for those seemingly contradictory results obtained with the baboons. According to these authors, it may be useful to distinguish between handedness and manual specialization. Handedness may be characterized by a consistent hand usage on familiar, highly practiced and relatively simple tasks, whereas manual specialization may concern novel, unpracticed and relatively complex tasks. This model suggests that manual preferences could be interpreted differently depending on the kind of tasks employed. For example, Young *et al.* argue that the manual specialization could be a better indicator of an underlying hemispheric specialization than handedness.

The reaching task can be conceived as a familiar and highly practised task. This is clearly not the case for the sliding panel tasks. Moreover, these last tasks require a precise movement. Given the kind of tasks we employed here and the results we obtained, we would like to suggest that the bimodal distribution of preferences with the board, the box and the hole corresponds to what Young *et al.* have called handedness. However, the unimodal distribution of preferences for the sliding panel tasks could correspond to a form of manual specialization. Since manual specialization can be viewed as a better indicator of hemispheric dominance than handedness, we can also hypothesize that this kind of preference may be more closely related to the neurofunctional asymmetries found with macaques and other nonhuman primates than the preferences for simple reaching (*op. cit.*).

Given that the reaching is a very practised activity, the symmetrical distribution of hand bias could be due, at least partially, to ontogenetic or experiential factors. By contrast, the sliding panel tasks were novel for the subjects and it is very unlikely that experience could have produced the hand preferences for these tasks. These baboons live in a semi-natural environment and consequently never had to manipulate objects such as solving sliding panel tasks before the present investigation. The left hand preference found for the six baboons to adjust the sliding panel could be viewed as the expression of a manual predisposition shared by the baboons; this predisposition is in turn likely to be related to an initial hemispheric asymmetry.

The sliding panel tasks can only be solved under the control of vision and these tasks possess in addition an obvious spatial component in the adjustments and alignments of the panel. We found, for this kind of task, the same left hand preference in gorillas [8] and baboons suggesting that this finding may have some generality in nonhuman primates.

Although the question is still largely open, there is a growing body of evidence to attribute some specific specializations to each side of the human brain [1]. If it is correct that spatial abilities (spatial localization, perception of spatial relations, production of spatial responses) characterize more the right than the left hemisphere in man [13, 21], it should then be of no

surprise to observe a left hand preference in gorillas and baboons to solve tasks with a heavy spatial load. This view is also consistent with Ettlenger's findings (*op. cit.*) of an initial preference for the left hand in visual discrimination tasks involving hand usage in monkeys and with the left hand preference observed in *Galago senegalensis* during food reaching [29, 30]. Although the present data might suggest an evolutionary continuum within human and non-human primates, additional studies will be needed to strengthen such conclusions.

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