

# Manual and Hemispheric Specialization in the Manipulation of a Joystick by Baboons (*Papio papio*)

Jacques Vauclair and Joël Fagot

Manual performance asymmetries were examined in 8 baboons (*Papio papio*). Using a joystick, monkeys had to track and hit with a cursor a randomly moving target on a monitor. The left or right hand was tested first, depending on group assignment, followed by a transfer to the other hand. A transfer effect is reported for the total number of trials to criterion and total number of successful trials. No effect was found for response time. However, for both test and transfer, the group initially tested with the left hand exhibited more controlled movements as demonstrated by shorter cursor's paths. Overall, it appears that the spatial components of the task are more sensitive to laterality effects than response times or learning scores.

The existence of functional asymmetries in nonhuman primates is now a central topic in the field of behavioral neurosciences. This field has been recently renewed by the perspectives offered by MacNeilage, Studdert-Kennedy, and Lindblom (1987). Those authors proposed that human laterality is rooted in the primate lineage and that population hand preferences already exist in nonhuman primates. With some exceptions (e.g., Boesch, 1991), recent evidence confirms the existence of manual lateralization at the group level in nonhuman primates. For example, in the motor domain, gibbons exhibited a left-hand preference in a mesh retrieval task and gorillas showed a right-hand preference (Olson, Ellis, & Nadler, 1990). In the perceptual domain, a left-hand preference was found in rhesus macaques for a haptic discrimination task (Fagot, Drea, & Wallen, 1991). Other evidence can be found in Ward and Hopkins (in press) and in Fagot and Vauclair (1991). The demonstration of manual preferences is congruent with other forms of hemispheric asymmetries, either at the functional (Hamilton & Vermeire, 1988) or anatomical level (Falk, Cheverud, Vannier, & Conroy, 1986).

Although these recent studies generally speak in favor of manual laterality in nonhuman primates, the available data are of little help to explain the asymmetry. As noted by Preilowski (1983) and Ettliger (1988), a major problem in the field of manual lateralization in nonhuman primates is that most of the studies (but see Hoerster & Ettliger, 1985) have measured hand preference only, that is the hand (left or right) the animal chooses. This kind of measure leaves untold whether the preferred hand is also the most efficient in terms of the biomechanical characteristics of the movements (e.g., spatial precision).

In our previous studies with nonhuman primates, we have demonstrated that manual preferences may be task dependent. For example, we have examined hand preferences of gorillas (*Gorilla gorilla*) and baboons (*Papio papio*) in a

visual-spatial task. In order to get a reward, the animal had to precisely align an opening made in a sliding panel with a fixed aperture in which food reinforcement was located. Both gorillas (Fagot & Vauclair, 1988a) and baboons (Fagot & Vauclair, 1988b) showed a significant left-hand preference in the adjusting phase of the task. However, no group preference emerged when the animals were tested on simple reaching for food. The above results led us to propose a distinction between the concept of handedness, which refers to preferences in simple and highly practiced activities, and the concept of manual specialization, which refers to preferences manifested in novel and highly controlled activities (Fagot & Vauclair, 1991). We have argued that only manually specialized tasks revealed consistent hemispheric asymmetry in the population under study.

This study is a continuation and extension of our previous visuospatial tasks in which we adopted a manual transfer procedure to assess the respective abilities of each hand. For that purpose, we developed a procedure with a videoformatted task that is partially similar to the one proposed by Richardson, Washburn, Hopkins, Savage-Rumbaugh, and Rumbaugh (1990). This method requires the fine manipulation of a joystick in order to bring into spatial correspondence two objects displayed on a monitor. This task allows the collection of data regarding both temporal and spatial hand performance.

## Method

### *Subjects*

Subjects were 8 juvenile Guinea baboons (*P. papio*), 4 males and 4 females, ranging from 3.5 to 7.0 kg. Baboons were wild caught and had never been involved in any experiment before this one. The animals lived as a social group of 14 baboons in an indoor-outdoor enclosure. They were never food deprived but received their daily rations of food after completion of the testing sessions.

### *Apparatus*

The apparatus consisted in an analog joystick (Measurement Systems, 521) connected, by an A-D converter (Data Translation board, DT 2801), to a PC-AT microcomputer and accompanying 14-in.

---

Jacques Vauclair and Joël Fagot, Cognitive Neuroscience Laboratory, Centre National de la Recherche Scientifique, Marseille, France.

Correspondence concerning this article should be addressed to Jacques Vauclair, Cognitive Neuroscience Laboratory, Centre National de la Recherche Scientifique, 31, chemin Joseph-Aiguier, 13402 Marseille cedex 9, France.

(35.56-cm) color monitor. As depicted in Figure 1, the apparatus also comprised an experimental cage (68 × 50 × 72 cm) equipped on its front with two handports and a viewport (8.7 × 8.0 cm). The monitor was in the longitudinal axis of the cage. Its screen was 47 cm from the cage front and was at eye level. The joystick, also in the longitudinal axis of the cage, was 18 cm from the front and 20 cm below the lower edge of the viewport. The apparatus was fitted with a food dispenser that provided 190-mg pellets on the floor of the cage.

### Procedure

The computer displayed on the screen both a red target and a green cursor (0.5 cm in diameter). Movements of the joystick in any direction resulted in isomorphic movements of the cursor on the screen. This isomorphism in movements concerned the direction of the cursor, its position on the screen and its speed. The task for the subject was to manipulate the joystick in order to hit the target with the cursor. A correct response required an accurate cursor-target collision that needed to be made within a time limit. Successful trials were always food reinforced and accompanied by a tone. Unsuccessful trials were followed by a raucous tone.

*Training period.* The shaping required a systematic manipulation of the degrees of freedom of the joystick movements. For that purpose, boards that contained different slots were fixed at the base of the joystick. These templates constrained movements of the stick. In the first shaping phase, movements were limited to the vertical axis with the target being displayed at either the top or bottom of the monitor. The subject had to respond upward when the target was located on the top and downward when the target was displayed on the bottom of the monitor. Mastery of that phase as well as of the following phases required 80% correct trials within 40 consecutive trials. When criterion level was reached, a novel template inducing horizontal movements (left-right) was used. In that second phase, the target was positioned either on the right or on the left of the cursor. In later phases, we combined vertical, horizontal, and diagonal paths. Finally, the template was removed to allow displacements of the cursor in any direction. During these shaping phases the targets were always

stationary and contacts between cursor and target needed to be made within 2 s. In the initial phases, targets were made of a large red square (6 × 6 cm). In the later phases, targets were smaller red squares (2 × 2 cm). Use of the right hand was initially imposed for 4 subjects, and the remaining 4 had to use their left hand. However, once monkeys had gone through the whole shaping process with one hand, they were immediately retrained to criterion with the other hand. This procedure was adopted in order to equilibrate the performance level of each hand before testing. It took 4–8 weeks (3 hr/day, 5 days/week) to train a monkey. Testing sessions followed immediately the shaping phases.

*Testing and transfer periods.* During testing and transfer periods, the computer displayed the cursor in the center of the screen and a target at a randomly determined location. The target was presented as a red ring (1.5 cm in diameter) that followed random erratic trajectories. The target was moving at a constant speed of approximately 2 cm/s. The animal had to move the joystick to track and hit the moving target within a time limit of 3 s. Each successful trial was rewarded. If the animal failed to hit the target within the 3-s period, the screen turned black and the trial was terminated. Regardless of the outcome of a given trial, the next trial was initiated after a 10-s intertrial interval.

The experiment was composed of one testing and one transfer period. In the testing period a given hand was used to manipulate the joystick. In the transfer period the performance of the other hand was evaluated. Subjects were assigned to two groups of 4 baboons each (2 males and 2 females). One group (Group L) was initially tested with the left hand, whereas the other was initially tested with the right hand. Subjects performed 16 series of 11 trials a day. Trials on which no joystick displacement was detected were not counted and were presented again. A delay of a minimum of 5 min separated two series of trials. Testing and transfer periods were terminated when subjects reached a criterion of 80% correct in 40 consecutive trials. The first trial of each series served as a warming trial and was omitted from the calculation of the performance level. In each trial the outcome of the joystick manipulation (success or failure) was automatically recorded. Moreover, the *x-y* coordinate of the cursor and the target were

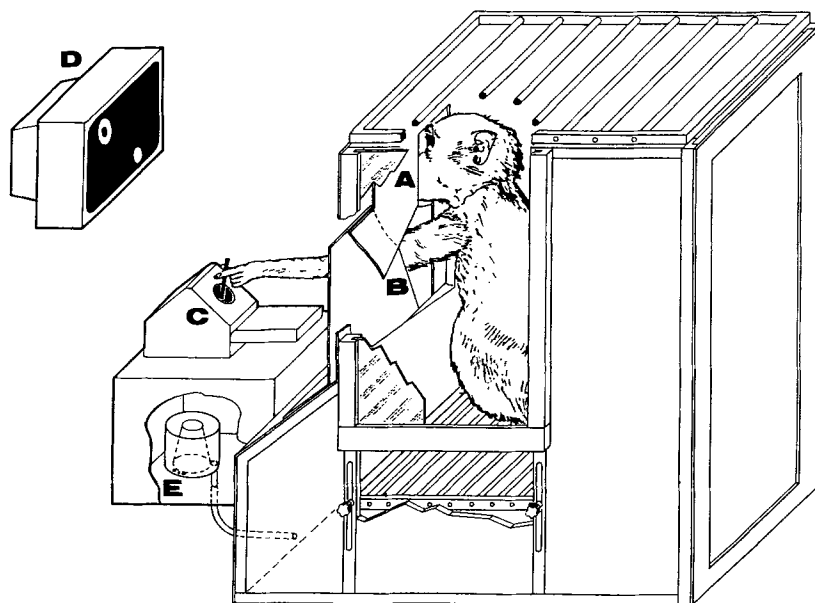


Figure 1. View of the apparatus showing the viewport (A), handports (B), joystick (C), monitor (D), and food dispenser (E).

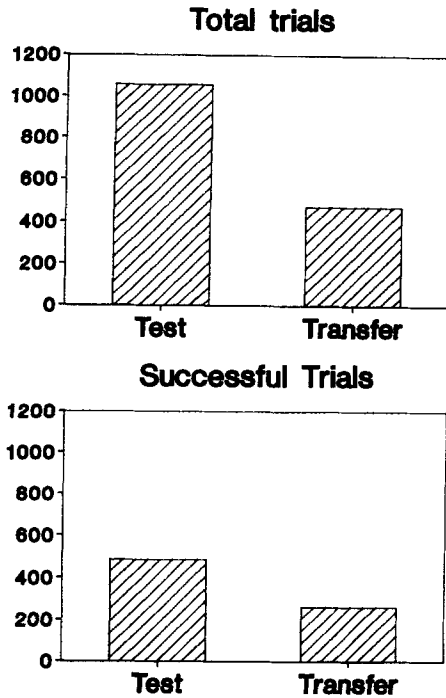


Figure 2. Mean number of total trials to criterion for test and transfer (top panel) and mean number of successful trials to criterion for test and transfer (bottom panel).

recorded every 100 ms. These data provided information regarding the path of the cursor.

The dependent variables of interest were for each hand: (a) the total number of trials to criterion, either successful or not; (b) the total number of successful trials to criterion; (c) the response time; and (d) the length of the trajectory of the cursor. The response time corresponded to the time elapsed (in milliseconds) between the cursor's first movement and its contact with target. The length of the path was computed by adding the distances covered by the cursor every 100 ms. The unit for length measurement was the pixel. Response time and length of the path were determined on successful trials only. Given the randomization of the location of target appearance on the screen, on some trials the target appeared in the vicinity of the cursor. Those trials had a different motor requirement because hitting the target was easy and needed no tracking movement. Thus, for the analyses of response time and length of path, trials in which the center of the target appeared at a position less than 100 pixels (i.e., less than 4 cm) from the cursor were neglected. These trials represented 13.2% of total trials.

For each dependent variable, an analysis of variance (ANOVA) was performed with the sex (male or female) and the group assignment (Group L or R) as the two between-subjects variables and the testing period (test or transfer) as the unique within-subjects variable. Moreover, correlational analyses were made to assess the dependency between the different variables.

## Results

### Number of Trials to Criterion

On average for Group L, the number of trials to reach criterion is equal to 1,099.5 ( $SD = 298.5$ ) and 310.2 ( $SD = 84$ ) for test and transfer, respectively. For Group R, these means

are equal to 1,014.5 ( $SD = 261.5$ ) and 633.2 ( $SD = 173.4$ ), respectively. An ANOVA performed on the total number of trials to criterion shows a significant testing period effect,  $F(1, 4) = 22.4$ ,  $p < .01$ . As shown in Figure 2 (top panel), the average number of trials to criterion was lower in the transfer period ( $M = 471.7$ ) than in the test period ( $M = 1,057.0$ ). This result demonstrates a positive intermanual transfer effect. No other effect or interaction reached significance.

For the group of 8 baboons, 48.8% of the trials were correct on average. The average numbers of successful trials to criterion for test and transfer periods were, respectively, 486 and 261. An ANOVA on the number of successful trials to criterion shows a transfer effect,  $F(1, 4) = 16.0$ ,  $p \leq .02$ , as the unique significant effect. That effect is depicted in Figure 2 (bottom panel).

### Response Time

Response times are 687.6 ms ( $SD = 89.3$ ) on average. Group L had a mean response time of 664.8 ms ( $SD = 112.9$ ). Response time for Group R was 710.3 ms ( $SD = 57.9$ ). An ANOVA on these data shows neither significant main effect nor significant interaction.

### Length of the Path

For the whole group of subjects, the average length of the cursor's trajectory was 527.4 pixels ( $SD = 126.0$ ). An ANOVA demonstrates a significant main effect of group,  $F(1, 4) = 68.9$ ,  $p = .001$ . This effect corresponds to a shorter path length in Group L ( $M = 431.5$ ,  $SD = 40.1$ ) than in Group R ( $M = 623.3$ ,  $SD = 107.4$ ). A main sex effect was also significant,  $F(1, 4) = 8.2$ ,  $p < .05$ . Males exhibited a shorter path on average ( $M = 494.4$ ,  $SD = 127.3$ ) than did females ( $M = 560.5$ ,  $SD = 124.4$ ). Those effects are shown in Figure 3. No other significant results emerged from this analysis.

### Correlational Analyses

Product-moment correlations were calculated between the different variables for both testing and transfer periods. These

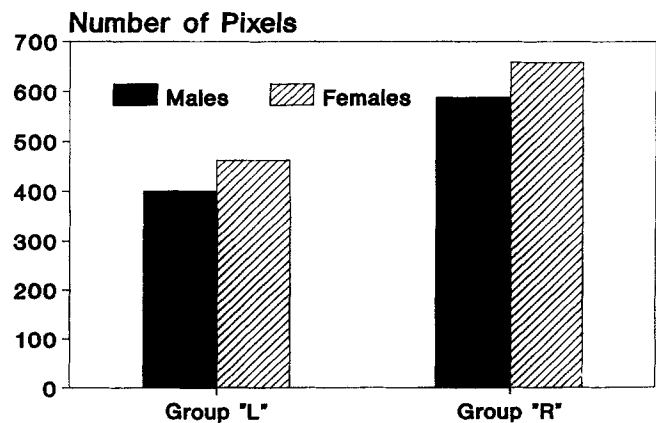


Figure 3. Mean length of cursor's trajectory as a function of sex and group.

correlations are reported in Tables 1 and 2. Total number of trials and the number of successful trials were highly correlated between testing and transfer. However, other correlations show no clear pattern between testing and transfer periods.

### Discussion

By way of joystick manipulation, 8 baboons had to hit with a cursor a target moving erratically on a monitor. Four monkeys were initially tested with their left hand and then with their right. The 4 others were tested in the reversed order. Hand performance was measured by the total number of trials to criterion, the total number of successful trials, response time, and trajectory of cursor. Two major results emerged. First, fewer trials were needed to reach criterion in the transfer than in the test period. Second, the subgroup tested first with the left hand (Group L) showed shorter trajectories' lengths than Group R.

The smaller number of trials to criterion (total and successful trials) when subjects were tested with the second hand clearly indicates a transfer effect. That effect is not evident for other measures of performance, such as response time and trajectory length. The observed benefit in the number of trials has already been described in other studies (Ebner & Myers, 1962; Hunter, Ettlinger, & Maccabe, 1975) with a tactile procedure for intact macaques. In contrast with our findings, lack of transfer in the number of trials to criterion has been reported by Preilowki, Reger, and Engele (1986). Those authors used a task that required monkeys to produce an isometric pressure of specific duration between the finger tips of the right or the left hand. However, this finger pressure task is different in nature from the tasks used in laterality studies because in the former task, movements of the fingers were very limited.

According to Brinkman and Kuypers (1973), distal movements are necessary to tap the functional advantages of the hemisphere contralateral to the hand used. Our videofor-matted task involved distal movements in the sense that the monkey had to grip and hold the joystick between the finger tips. However, arm movements were not physically restricted. Thus, one cannot definitively rule out the possibility of an activation or control of the hemisphere ipsilateral to the hand used. Altogether, given the distal components of the joystick task and the involvement of fine movements, it is presumed that this activity is essentially under the control of the hemisphere opposite to the hand used.

Table 1  
*Matrix of Product-Moment Correlations for the Test Period*

| Variable                                | 1    | 2   | 3    |
|---|------|-----|------|
| 1. Total trials to criterion            | —    |     |      |
| 2. Total successful trials to criterion | .93* | —   |      |
| 3. Response time                        | .09  | .38 | —    |
| 4. Length of the path                   | .10  | .41 | .73* |

\* $p < .05$ .

Table 2  
*Matrix of Product-Moment Correlations for the Transfer Period*

| Variable                                | 1    | 2    | 3   |
|---|------|------|-----|
| 1. Total trials to criterion            | —    |      |     |
| 2. Total successful trials to criterion | .98* | —    |     |
| 3. Response time                        | -.34 | -.46 | —   |
| 4. Length of the path                   | .72* | .65  | .04 |

\* $p < .05$ .

In average for test and transfer, Group L had shorter paths than Group R. This difference indicates that hand movements in Group L were more controlled than movements in Group R. Considering testing only, path differences between groups suggest a specialization of the right hemisphere. However, the right hemisphere specialization hypothesis does not account for the data obtained in the transfer because, during transfer, Group L maintained an advantage in terms of path even though subjects used their right hand. It is suggested that, during the testing period, both groups adopted a strategy that was kept during transfer.

Group effects were observed for path but not for response time. This finding may be explained by monkeys' behaviors in chasing the moving target. Two kinds of hitting strategies were seen. The first involved an almost straight cursor's path from the center of the screen to the target's location. That hitting strategy required very few regulatory movements but an anticipation of the target's movements. By contrast, the second strategy used very rapid corrective movements of a wide amplitude. This strategy appeared when the cursor missed its target during the first hitting attempt (corresponding to the first strategy). In that case, the subject moved its cursor away from the target and then triggered its movement toward it. Thus, intertrials differences were mostly due to path differences rather than response times. These important variations in path versus response time may explain the absence of systematic significant correlations between the two measures as well as the greater sensitivity of the path to hand strategy.

Another published study has examined manual performance in chimpanzees and rhesus monkeys manipulating a joystick to direct a collision on a monitor between a moving target and a cursor (Hopkins, Washburn, & Rumbaugh, 1989). Hopkins et al. reported systematic response times for the right hand in all their subjects. We did not find similar results in baboons. It seems to us that these differences lie in the nature of the isomorphism between cursor and joystick displacements used in the two experiments. In our study the isomorphism was total in terms of direction, position, and speed. In the system used by Hopkins et al., when the joystick returned to the center position, the cursor remained in the same location on the screen until the joystick was again manipulated (Richardson et al., 1990). Also, there was only a directional isomorphism, and the cursor moved at a constant velocity regardless of the speed of the joystick's displacements. This is reflected by response times that were more than four times greater in the study by Hopkins et al. (3.25 s on average) than in ours (0.7 s). Two other differences with regard to shaping procedures may

explain the discrepancies in results between our study and Hopkins et al.'s study. First, we restricted movements of the joystick by using templates. Second, we selected the hand used during shaping and testing, whereas Hopkins et al. initially let the animal use its preferred hand. We suggest that these procedural dissimilarities affected the motor and perceptual components of the tasks and consequently the observed hemispheric asymmetry.

A chief conclusion of this study is that path was more sensitive to laterality effects than response time and number of trials to criterion. To us, path provides a better picture of the strategy used by the subject than the other aforementioned variables, which constitute more global indicators of performance. It is suggested that more systematic usage of this kind of variable may help clarify the nature of hemispheric specialization and the relationship between hand preference and hand performance.

### References

- Brinkman, C., & Kuypers, H. G. J. M. (1973). Cerebral control of contralateral and ipsilateral arm, hand and finger movements in the split-brain rhesus monkey. *Brain*, *96*, 653-674.
- Boesch, C. H. (1991). Handedness in wild chimpanzees. *International Journal of Primatology*, *12*, 541-558.
- Ebner, F. F., & Myers, R. E. (1962). Direct and transcallosal induction of touch memories in the monkey. *Science*, *138*, 51-52.
- Ettlinger, G. (1988). Hand preference, ability and hemispheric specialization: In how far are these factors related in monkeys. *Cortex*, *24*, 389-398.
- Falk, D., Cheverud, J., Vannier, M. W., & Conroy, G. D. (1986). Advanced computer graphics technology reveals cortical asymmetry in endocasts of rhesus monkeys. *Folia Primatologica*, *46*, 98-103.
- Fagot, J., Drea, C., & Wallen, K. (1991). Asymmetrical hand usage in rhesus monkeys (*Macaca mulatta*) in tactually and visually regulated tasks. *Journal of Comparative Psychology*, *105*, 260-268.
- Fagot, J., & Vauclair, J. (1988a). Handedness and bimanual coordination in the lowland gorilla. *Brain Behavior and Evolution*, *32*, 89-95.
- Fagot, J., & Vauclair, J. (1988b). Handedness and manual specialization in the baboon. *Neuropsychologia*, *26*, 795-804.
- Fagot, J., & Vauclair, J. (1991). Manual laterality in nonhuman primates: A distinction between handedness and manual specialization. *Psychological Bulletin*, *109*, 76-89.
- Hamilton, C. R., & Vermeire, B. A. (1988). Complementary hemispheric specialization in monkeys. *Science*, *242*, 1691-1694.
- Hoerster, W., & Ettlinger, G. (1985). An association between hand preference and tactile discrimination performance in the rhesus monkey. *Neuropsychologia*, *23*, 411-413.
- Hopkins, W. D., Washburn, D. A., & Rumbaugh, D. M. (1989). Note on hand use in the manipulation of joysticks by rhesus monkeys (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *103*, 91-94.
- Hunter, M., Ettlinger, G., & Maccabe, J. J. (1975). Intermanual transfer in the monkey as a function of amount of callosal sparing. *Brain Research*, *93*, 223-240.
- MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *The Behavioral and Brain Sciences*, *10*, 247-303.
- Olson, D. A., Ellis, J. E., & Nadler, R. D. (1990). Hand preferences in captive gorillas, orang-utans and gibbons. *American Journal of Primatology*, *20*, 83-94.
- Preilowski, B. (1983). Is there a hemispheric specialization in nonhuman primates? In P. K. Seth (Ed.), *Perspectives in primate biology* (pp. 109-117). New Delhi: Today's and Tomorrow's Printers and Publishers.
- Preilowski, B., Reger, M., & Engele, H. C. (1986). Handedness and cerebral asymmetry in nonhuman primates. In D. M. Taub & F. A. King (Eds.), *Current perspectives in primate biology* (pp. 270-282). New York: Van Nostrand Reinhold.
- Richardson, W. K., Washburn, D. A., Hopkins, W. D., Savage-Rumbaugh, E. S., & Rumbaugh, D. M. (1990). The NASA/LRC computerized test system. *Behavior, Research Methods, Instruments, & Computers*, *22*, 127-131.
- Ward, J. P., & Hopkins, W. D. (in press). *Primate laterality: Current behavioral evidence of primate asymmetries*. New York: Springer Verlag.

Received March 19, 1992

Revision received July 28, 1992

Accepted September 8, 1992 ■