Manual Laterality in Nonhuman Primates: A Distinction Between Handedness and Manual Specialization

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This article examines individual and group manual lateralization in nonhuman primates as a function of task's demands. It is suggested to distinguish low- from high-level manual activities with respect to the novelty variable and to the spatiotemporal scale of the movements. This review shows that low-level tasks lead to (a) symmetrical distributions of hand biases for the group and (b) manual preferences that are not indicative of the specialization of the contralateral hemisphere. In contrast, behaviors expressed in high-level tasks (a) show asymmetrical distribution of hand biases for the group and (b) seem to be related to a specialization of the contralateral hemisphere. Two types of lateralization, handedness and manual specialization, correspond to the 2 levels of tasks that are distinguished.

In the past 20 years, many studies have been done to investigate the manual (or paw) preferences in nonhuman primates (e.g., Marchant & Steklis, 1986; Sanford, Guin, & Ward, 1984; Vauclair & Fagot, 1987a) and other mammals such as cats (Warren, Abplanalp, & Warren, 1967) or mice (Collins, 1975; Papaioannou, 1972). The primary purpose of these studies was to determine whether animals possess asymmetrical forms of cerebral organization analogous or possibly homologous to those found in humans. The search for a possible precursor of human hemispheric specialization in animals was primarily focused on nonhuman primates because of their phylogenetic proximity to humans. Under the assumption that manual preferences might be a good index of the functional asymmetries of the cerebral hemispheres, researchers made attempts to describe manual lateralization in nonhuman primates by addressing the following questions: Are individuals lateralized for a given task? Are the preferences observed for different tasks consistent? How are biases distributed in the group under study and, more generally, in the species? Are there any differences between taxons (new-world monkeys, old-world monkeys, apes, and humans)? Is there an evolutionary continuum among animal species and between animals and humans?

To answer these questions, investigators can study either hand preference or hand performance asymmetries. With respect to the manual preference paradigm, repetitive presentations of a given task (e.g., reaching for food) produce individual scores of right- and left-hand uses. The strength and the bias of individual manual lateralization can then be derived. The strength is obtained by calculating the deviation from a random 50% hand usage regardless of the hand preferred (e.g., absolute value of the difference between the percentage of right-hand uses and 50%). Bias refers to the direction of manual preference (left or right). Statistical analyses, such as chi-square, of the number of left- versus right-hand uses allow classification of individuals as right-, left-, or nonasymmetrical hand users. In the manual performance paradigm, individual hand performance is measured on some dimension (e.g., reaction time or accuracy) as subjects solve the same task with each hand. Individuals are classified as right- or left-handers when one hand is shown statistically to perform better on average than the other.

For both paradigms, distribution of individual lateralities for the sample or population under study can be either asymmetrical, when one hand bias outnumbers the other, or symmetrical, when there is no significant difference between the number of left- and right-handers. Actually, the aforementioned procedures used with nonhuman primates gave rise to a heterogeneous picture of their manual lateralization which, in turn, has led to various analyses and interpretations. To present the current state of our knowledge, we will examine the frameworks proposed by Warren (1980) and by MacNeilage, Studdert-Kennedy, and Lindblom (1987).

Warren's (1980) analyses are based on an extensive series of behavioral and neuropsychological studies with old-world monkeys (Warren, 1953, 1977; Warren et al., 1967; Warren & Nonneman, 1976). Following a reinterpretation of several sets of data accumulated before 1980, Warren has described manual preferences observed in nonhuman primates as being: (a) symmetrically distributed in the population with no significant dif-

ference between the number of left- and right-handers, (b) dependent on the task and other situational constraints (e.g., Deuel & Dunlop, 1980), (c) dependent on practice and learning, and (d) independent of other lateralized functions in monkeys (e.g., the processing of acoustic signals). Henceforth, Warren conceived manual laterality in monkeys as being "primarily the result of experience, and not the expression of any organismic asymmetry" (Warren, 1977, p. 169). Moreover, Warren extended his position to hemispheric lateralization and concluded that "the several types of cerebral laterality observed in nonhuman species are most probably analogous rather than homologous to the functional specification of the hemispheres in man" (Warren, 1980, p. 357).

Warren's position can be criticized on several grounds. His view only accounts for symmetrical distributions, that is, when the number of right-handers is not statistically different from the number of left-handers. However, except by reference to methodological artifacts, Warren's position is unable to account for the current evidence of a population level hand asymmetry in nonhuman primates (see references later in the text). Moreover, Warren's position cannot explain asymmetrical distributions in the absence of environmental constraints, particularly, as noted by MacNeilage et al. (1987), when such distributions are observed in field studies (Itani, 1957; Yuanye, Yunfen, & Ziyun, 1986) or in laboratory studies with naive subjects (e.g., Ettlinger, 1961; Sanford et al, 1984; Fagot & Vauclair, 1988b). In addition, contrary to Warren's view of an independence of hand laterality from hemispheric asymmetries, some recent studies have demonstrated a relationship between: (a) manual preferences and the effects of specific lesions in the contralateral hemisphere (Garcha, Ettlinger, & Maccabe, 1980, 1982) and (b) the hand preferred and competency of each hemisphere in a visual discrimination task (Hamilton & Vermeire, 1982).

The conceptions of MacNeilage, Studdert-Kennedy, and Lindblom (1987) are markedly different from Warren's position. These authors view the previous inconclusive results about nonhuman primate manual lateralization as largely due to several effects, such as the use of animals too young to express a stable preference and tasks inadequate to demonstrate hand laterality. When these factors are considered, MacNeilage et al. (1987) give evidence of several instances of asymmetrical preference distributions in nonhuman primates. In prosimians, a left-hand preference emerged for visually guided movements accompanied by a specialization for postural support involving the right upper limb. The asymmetry in favor of the left hand remains present in monkeys and possibly in apes along with a right-hand specialization for manipulation and bimanual coordination. This right-hand specialization may have evolved between prosimians and humans "from the postural specialization with the development of the opposable thumb, and decreasing demands on the right limb to support vertical posture in monkeys" (MacNeilage et al., 1987, p. 247). Thus, with regard to MacNeilage et al.'s theory, a population level left-hand preference is expected for visually guided activities in prosimians, monkeys, and may be for apes. The authors postulate that this preference should arise beyond a certain minimum demand level. Although they are a bit vague about that threshold, they argue that the left-hand preference may be evoked (a) when the task has a low manipulatory requirement (single act) be-

cause complex manipulative tasks (multiple acts) elicit a right hand preference,[1] (b) in field situations rather than in laboratory settings, and (c) with adult subjects rather than with young.

From the perspective proposed by MacNeilage et al. (1987), one could expect that the task of simple reaching for food induces a left-hand preference because it strongly depends on vision, both for the initiation of the "open-loop" ballistic transport of the arm and for the final "close-loop" control of the movement (Paillard & Beaubaton, 1975). Moreover, the task of simple reaching for food has little manipulative load and only implies a single motor act. Actually, MacNeilage et al. (1987) recognized that such a task might induce a left-hand preference when the field and age conditions are respected.[2]

Table 1 gathers the largest available sample of studies concerned with food-reaching activities in nonhuman primates. Only studies that used an experimental procedure not deliberately conducive to preference for a particular hand are included in Table 1. For example, Lehman (1980b) is not included because the hand opposite the preferred one was systematically rewarded. Previous reaching experiments have shown that different distributions of preferential biases may appear depending on the posture of the animal (vertical vs. horizontal stance, Sanford et al., 1984) and on the type of reaching (extreme extension vs. slight extension of the limbs, Forsythe, Milliken, Stafford, & Ward, 1988; catching in mid air vs. reaching on the floor, Tokuda, 1969, which included the data of Kawai's monkeys, 1967). Catching, reaching executed in a vertical stance, or reaching performed with an extreme extension of limbs are thus excluded from Table 1. These actions will be examined later because they are assumed to be functionally distinct from the task of simple reaching for food.

Among the 48 samples of primates that were tested for food

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[1] MacNeilage et al. (1987) often use the concepts of "complexity," "task demand," and "manipulation" without providing a comprehensive definition. To discuss the studies of old-world monkeys, they proposed a classification of manual tasks (p. 248) that rests on a move from "simple reach tasks," involving picking up single food items presented alone on flat surfaces, to "complex" manipulative and reaching tasks. A typical complex task involves one or more hasps being opened. The underlying criterion of their classification is the number of acts preceding the "terminal act" of food reaching. Further into the text, they seem to assimilate the "manipulative demand" to the use of serial movements but they do not really emphasize the precision level involved in each movement. In the present article, complexity is defined in terms of the movement precision, relative to the spatiotemporal dimension of the task.

[2] Living conditions (field vs. lab) are considered by MacNeilage et al. (1987) as an important variable for the appearance of hand asymmetry. They present reaching in the field as follows: "the food can be placed anywhere in a 360° field and at various distances from the monkey" (p. 257). This situation is contrasted with laboratory studies in which "a food item is placed in one of a small number of locations in front of the cage" (p. 257). If we follow the authors, the opposition field/laboratory corresponds in fact to free reaching versus restricted or standardized reaching. Such a distinction implies that reaching performed in a large cage where the subject is free to move can have the same characteristics as reachings in the field. It appears to us that restricted versus free reaching is more appropriate than field versus laboratory and still fits with the distinction proposed by MacNeilage et al.

Table 1

Summary of the Studies on Simple Reaching for Food in Nonhuman Primates

Study	Species	Condition[a]	Age	Criterion[b]	Right	Left	No preference	Statistics[c]	
Forsythe & Ward (1988)	*Lemur macaco*	Free	A + Y	Z score	12	20	1	$\chi^2 = 2$	ns
Milliken, Forsythe, & Ward (1989)	*Lemur catta*	Free	A + Y	Z score	3	7	3	bin	ns
Ward et al. (1990)	*Lemur catta*	Free	A + Y	Z score	14	21	7	$\chi^2 = 1.4$	ns
Ward et al. (1990)	*Lemur coronatus*	Free	A + Y	Z score	4	6	1	bin	ns
Ward et al. (1990)	*Lemur macaco*	Free	A + Y	Z score	7	19	3	$\chi^2 = 5.4$	p < .05
Ward et al. (1990)	*Lemur mongoz*	Free	A + Y	Z score	12	9	5	$\chi^2 = 0.4$	ns
Ward et al. (1990)	*Lemur rubriventer*	Free	A + Y	Z score	4	1	0	—	—
Ward et al. (1990)	*Lemur fulvus a.*	Free	A + Y	Z score	5	6	4	$\chi^2 = 0.1$	ns
Ward et al. (1990)	*Lemur fulvus c.*	Free	A + Y	Z score	5	15	4	$\chi^2 = 5$	p < .05
Ward et al. (1990)	*Lemur fulvus f.*	Free	A + Y	Z score	5	3	3	bin	ns
Ward et al. (1990)	*Lemur fulvus r.*	Free	A + Y	Z score	3	8	3	$\chi^2 = 2.3$	ns
Ward et al. (1990)	*Lemur fulvus s.*	Free	A + Y	Z score	6	3	8	bin	ns
Forsythe, Milliken, Stafford, & Ward (1988)	*Varecia variegata*	Free	?	Z score	0	1	4	—	—
Sanford, Guin, & Ward (1984)	*Galago senegalensis*	Restricted	A	60%	5	7	0	$\chi^2 = .33$	ns
Fragaszy & Mitchell (1990)	*Cebus apella*	Free	A	$\chi^2, p < .05$	1	3	3	—	—
Box (1977)	*Callithrix jacchus*	Free	A + Y	$\chi^2, p < .05$[d]	1	6	1	bin	ns
Hall & Mayer (1966)	*Erythrocebus patas*	Restricted	A + Y	50% + 2 σ	4	3	1	bin	ns
Yuanye, Yunfen, & Ziyun (1986)	*Rhinopithecus*	?	?	?	5	2	1	bin	ns
Yuanye et al. (1986)	*Presbytis*	?	?	?	10	3	3	$\chi^2 = 3.77$	p < .1
Brooker, Lehman, Heinbuch, & Kidd (1981)	*Macaca radiata*	Free	A + Y	$\chi^2, p < .05$	22	21	24	$\chi^2 = 0.02$	ns
Franz (1913)	*Macaca mulatta*	Restricted	?	$\chi^2, p < .05$[d]	0	3	3	—	—
Warren (1953)	*Macaca mulatta*	Restricted	A + Y	80%	27	26	31	$\chi^2 = 0$	ns
Cole (1957)	*Macaca mulatta*	Restricted	?	?	8	5	0	$\chi^2 = 0.69$	ns
Brookshire & Warren (1962)	*Macaca mulatta*	Restricted	Y	50% + 3 σ	5	12	2	$\chi^2 = 2.88$	p < .1
Lehman (1970)	*Macaca mulatta*	Restricted	Y	50%	11	12	1	$\chi^2 = 0.04$	ns
Lehman (1978)	*Macaca mulatta*	Restricted	A + Y	50%	80	91	0	$\chi^2 = 0.71$	ns
Lehman (1980c)	*Macaca mulatta*	Restricted	Y	50%	%R = 50.5 for the group (N = 38)			—	—
Deuel & Dunlop (1980)[e]	*Macaca mulatta*	Restricted	A	70%	5	8	19	$\chi^2 = 0.69$	ns
Deuel & Dunlop (1980)[f]	*Macaca mulatta*	Restricted	A	70%	8	2	5	bin	ns
Hamilton (personal communication, April 1988)	*Macaca mulatta*	Restricted	Y	HI > 33.3[g]	20	21	14	$\chi^2 = 0$	ns
Fagot, Drea, & Wallen (in press)	*Macaca mulatta*	Free	A + Y	G test, p < .05	12	15	24	$\chi^2 = 0.03$	ns
Itani (1957)	*Macaca fuscata*	Free	A + Y	80%[h]	16	30	23	$\chi^2 = 4.26$	p < .05
Itani, Tokuda, Furaya, Kano, & Shin (1963)	*Macaca fuscata*	Free	A + Y	?	118	149	127	$\chi^2 = 3.6$	p < .1
Furaya, in Itani et al. (1963)	*Macaca fuscata*	Free	?	?	38	37	36	$\chi^2 = 0.01$	ns
Tokuda (1969)	*Macaca fascata*	Free	A + Y	80%	8	17	16	$\chi^2 = 3.24$	p < .1
Lehman (1980a)	*Macaca fascicularis*	Restricted	Y	50%	35	23	0	$\chi^2 = 2.48$	ns
Deuel & Shaffer (1987)	*Macaca fascicularis*	Restricted	Y	70%	10	5	22	$\chi^2 = 1.67$	ns
Beck & Barton (1972)	*Macaca arctoides*	Restricted	Y	50% + 3 σ	5	2	3	bin	ns
Cole (1957)	*Macaca nemestrina*	Restricted	?	?	10	6	0	$\chi^2 = 1$	ns
Cole (1957)	*Papio furax*	Restricted	?	?	1	3	0	—	—
Ross, Wilczynski, & Albert (1987)	*Papio cynocephalus*	Free	?	?	11	17	0	$\chi^2 = 1.2$	ns
Vauclair & Fagot (1987b)	*Papio papio*	Free	A	$\chi^2, p < .05$	7	2	2	bin	ns
Fagot & Vauclair (1988a)	*Gorilla gorilla*	Free	A + Y	$\chi^2, p < .05$	3	3	4	bin	ns

Table 1 (continued)

Study	Species	Condition[a]	Age	Criterion[b]	Right	Left	No preference	Statistics[c]	
Olson, Ellis, & Nadler (1990)	Gorilla gorilla	Free	A + Y	$\chi^2, p < .05$	5	2	5	bin	ns
Olson et al. (1990)	Pongo pygmaeus	Free	A + Y	$\chi^2, p < .05$	4	3	5	bin	ns
Olson et al. (1990)	Hylobates lar	Free	A + Y	$\chi^2, p < .05$	2	6	0	bin	ns
Marchant & Steklis (1986)	Pan troglodytes	Restricted	A + Y	$\chi^2, p < .001$	3	1	1	—	—
Steklis & Marchant (1987)	Pan troglodytes	Free	?	$\chi^2, p < ?$	10	11	5	$\chi^2 = 0.05$	ns

Note. A = adult; Y = young; ? = information not provided in the original paper.
[a] Testing condition refers to the distinction between free versus restricted reachings (cf. Footnote b). [b] Criterion or statistical test chosen in the study to establish individual preferences. [c] To check the distribution of left- versus right-handers, we used a binomial two-tailed test when $5 < N = < 10$, or a chi-square when $N > 10$. [d] Because of a lack of information concerning criteria used in the study, a chi-square test was performed on the individual data. [e] Monkeys were tested in a primate chair. [f] Monkeys were tested in a Wisconsin General Test Apparatus. [g] $HI = 100(R - L)/(R + L)$. [h] The criterion was 80 consecutive reaches or more with the same hand.

reaching, 41 allowed statistical analyses ($N > 6$, see Table 1). Three studies indicated a tendency ($p = < .10$) for a left-hand preference (Brookshire & Warren, 1962; Itani, Tokuda, Furaya, Kano, & Shin, 1963; Tokuda, 1969). One study (Yuanye et al., 1986) found a tendency in favor of the right hand. Three samples were significantly left biased (Lemur macaco and Lemur fulvus coronatus, Ward et al., 1990; and Macaca fuscata, Itani, 1957).[3] None were significantly right biased. Thus, the vast majority of these studies (38 out of 41) provided no significant evidence for any sort of group hand asymmetry. Among the 28 samples of primates that have been tested in a setup implying no movement constraint, (free condition, cf. footnote 2), 3 have demonstrated a preference for one side (Itani, 1957, and 2 samples in Ward et al., 1990). The 25 others failed to elicit a significant population level preference. With regard to the argument that animal age is an important variable that was posited by MacNeilage et al. (1987), none of the studies conducted with adult subjects has shown a population level preference (e.g., Deuel & Dunlop, 1980). Additional evidence against the hypothesis for left-hand food reaching can be found in Vauclair and Fagot's (1987b) study that found no left-hand preference in adult baboons tested in a field situation. In short, with respect to the age and setting condition (free vs. restricted) criteria advanced by MacNeilage et al., data on reaching for food do not support the assumption of a left-hand preference for visually guided activities.

The generality of a right-hand preference for manipulative tasks can also be questioned. Indeed, MacNeilage et al. (1987) admitted that several studies failed to show asymmetries in tasks involving manipulations of diverse kinds of boxes (Brookshire & Warren, 1962; Cole, 1957; Trevarthen, 1978; Warren, 1977). Several other examples counter to the right-hand preference can be found in studies with apes (Fagot & Vauclair, 1988a; O'Neil, Stratton, Ingersoll, & Fouts, 1978), monkeys (Fagot & Vauclair, 1988b; Hamilton, 1990), and new-world monkeys (Fragaszy & Mitchell, 1990).

In the following sections, we will propose a perspective that has the advantage of explaining a large number of results concerning the symmetry or asymmetry of hand preference in nonhuman primate species. We will provide an analysis of the distributions of manual preferences as a function of task require-

ments that will lead us to suggest that the coexistence of symmetrical and asymmetrical distributions within primates' hand preferences is not the result of methodological artifacts but rather corresponds to two distinct expressions of hand usage related to the type of task used.

Factors Expected to Affect Manual Laterality

Although neuropsychological studies have demonstrated many instances of cerebral lateralization in humans, the traditional dichotomies (e.g., verbal/nonverbal, analytic/hollistic) advanced to account for these asymmetries now appear inadequate. Recent reviews have rejected the idea of a strict dichotomy between the hemispheres (Beaumont, Young, & McManus, 1984) and have considered differences in hemispheric functions as being not only qualitative but also quantitative (Bradshaw & Nettleton, 1981; Sergent, 1982b). In this line of thought, Zaidel (1983), followed by Bruyer (1986), argued in favor of a model of "relative specialization" versus "exclusive specialization." In contrast with the model of exclusive specialization, relative specialization acknowledges that some tasks can be performed by both hemispheres, although not necessarily with equal competence. For hand usage, we could infer that both hands (or hemispheres) could possess the basic abilities to perform some tasks, but only one hand (or hemisphere) should be able to perform other more demanding tasks. Thus, the failure to demonstrate manual asymmetries for a given task may only reflect the inadequacy of the task to reveal the asymmetry. Recent approaches (e.g., Healey, Liederman, & Geschwind, 1986) that conceive manual preferences in man as not being reducible to a "unidimensional trait" are congruent with that position.

In the context of human manual laterality, several factors affect the distribution of hand biases. These factors concern either the cognitive treatment of the task (e.g., Nachson & Carmon, 1975) or its motor requirement (i.e., muscular segments

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[3] Regarding to Itani's study, it should be noted that the author used food incentives of very small size (grains of wheat) that most certainly elicited very precise reaching movements.

involved, e.g., proximal or distal; Healey et al., 1986). According to Healey et al. (1986) and Steenhuis & Bryden (1989), the factors related to the skillfulness of the task are of particular importance, and the more skilled actions the task requires, the stronger the bias at the population level. This dimension of hand preference can be evaluated through the temporal and spatial characteristics of the movement. Studies on humans have revealed that hand laterality is differentially affected by variations in the temporal (Flowers, 1975; Nakamura & Saito, 1974; Todor & Smiley, 1985; Sheridan, 1973) or in the spatial requirements of the task (Annett et al., 1979; Flowers, 1975; Steingrueber, 1975; Todor & Smiley, 1985). For example, it has been shown that object size affected lateral preferences in right-handed adults performing a mere reaching task (only 58% of right-handed subjects used their right hand to pick up a large ball; Harris & Carlson, 1988). The action of picking up an object also appears to be less lateralized than other skilled activities such as using tools or sewing (Steenhuis & Bryden, 1989). In a task requiring rapid movements of a stylus between two targets with either the left or right hand, the performance (velocity) of the left hand was more affected by a decrease in the target size than that of the right hand (Todor & Smiley, 1985). The spatial and temporal characteristics of a given task might not be independent of one another because movements realized in a fine temporal scale generally require a fine spatial scale (Guiard, 1987).

Initial execution of a novel voluntary movement implies the intervention of specific attentional and cognitive processes. With practice, a motor program is progressively established. According to Paillard (1986), the acquisition phase and the final phase after consolidation of fine motor skills might be mediated by different neural routes, as suggested by the differential effect of a bilateral pyramidotomy on highly practiced versus newly acquired skills. In a more cognitive perspective (e.g., in the treatment of linguistic information), it has been argued that hemispheres are differently specialized to process novel versus practiced, well-routinized tasks (Goldberg & Costa, 1981). Specifically, the authors suggest that "the right hemisphere plays a critical role in initial stages of acquisition, whereas the left hemisphere is superior in utilizing well-routinized codes" (Goldberg & Costa, 1981, p. 144). Furthermore, familiarity and practice factors have been evoked to account for observed switches from right hemisphere processing to left hemisphere processing in laterality tasks (for face recognition see Damasio, 1989, and Ross-Kossak & Turkewitz, 1984; for other visual stimuli, see Hellige, 1976; Kittler, Turkewitz, & Goldberg, 1989; and Sergent, 1982a). For human manual laterality, novelty has been shown to affect the performance of each hand in a tactile discrimination task (Streitfeld, 1985). In this study, the author showed a left-hand/right-hemisphere advantage in judging tactually presented lines. This asymmetry was present only in the first block of 30 trials but disappeared for the second block. Moreover, the practice affects the performance of each hand (e.g., Perelle, Ehrman, & Manowitz, 1981). Distributions of manual preferences also change with age in childhood (Young, 1990) and in adulthood (Fleminger, Dalton, & Standage, 1977; Weller & Latimer-Sayer, 1985).

The aforementioned variables that refer to both motor (e.g., muscular mobilization) and cognitive (e.g., attentional pro-

cesses) aspects of the task affect human lateralization. We thus believe it is useful to consider them in the assessment of manipulative tasks and in the interpretation of the data obtained with nonhuman primates. Although several authors (e.g., MacNeilage, 1987; Preilowski, 1983) have stressed the necessity of considering task characteristics, the analyses provided so far have not taken into account the variables mentioned here.

For our current purpose, we will define and then classify tasks according to two broad categories: high-level tasks and low-level tasks. High-level tasks imply finely tuned motor actions because of the spatiotemporal dimensions of the movement required or cognitively complex activities involved (or both) due notably to the characteristic of novelty.[4] By contrast, low-level tasks concern grossly regulated activities or familiar, practiced activities, or both. This latter feature would imply that these activities would be less demanding in terms of cognitive processes (e.g., attentional requirements). We recognize that the use of a dichotomic classification only roughly accounts for the distribution of continuous variables such as novelty/practice and the spatiotemporal dimensions of the movement. Although this dichotomy is preliminary, we consider it useful at this stage given the current state of our knowledge. However, the reader should keep in mind that this dichotomy represents a minimal classification of a graded continuum.

Because human manual activities implying motor precision as well as cognitive complexity generally lead to a preference at the group level, and under the assumption that both hemispheres share common competencies (cf., e.g., Zaidel's model, 1983), we now expect that high-level but not low-level tasks represent the best situations to tap functional features of one hemisphere. Moreover, only high-level tasks should produce asymmetry in the distribution of lateral biases (left or right), both at the hemispheric and behavioral levels. By contrast, low-level tasks are not necessarily expected to induce a consistency of biases at the group level.

There are several implications in considering these factors (spatiotemporal dimension and novelty) for nonhuman primates hand laterality. First, because only high-level tasks should reveal hemispheric specialization, calculating average preferences over different tasks without taking into account the nature and the features of the tasks (e.g., Finch, 1941) could mask asymmetry, both for individuals and for groups. Second, the motor difficulty of a given task with respect to its temporal and spatial characteristics must be evaluated with reference to the manipulative abilities of the species that may depend, for example, on the anatomical divergence of the thumb from the other digits (Napier, 1961; Reynolds, 1975). In this respect, it is questionable to sum up data collected on different species in

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[4] Novelty can be defined in at least two ways: movement novelty or situation novelty. Movement novelty could describe the use of a new set of movements in a given context. Situation novelty could describe the application of a set of movements to a context slightly different from the one on which it was originally applied (e.g., picking up food on the ground or picking up food in a food well). Given the difficulty to experimentally dissociate these two aspects, one can only suggest cases or situations which should optimize novelty, namely through the first appearance of a behavior in ontogeny or in a situation that is the more distant from routine movements and familiar contexts.

order to determine distribution of hand preferences. Third, we can consider the picking up of food on a flat surface, a highly practiced task par excellence, as the prototype of a low-level task, at least for the most manipulative species. The same is true for other gross motor actions such as pulling, holding, or routine daily activities (e.g., Brooker, Lehman, Heinbuch, & Kidd, 1981; Vauclair & Fagot, 1987a). Conversely, assuming that the task is understood by the subject, initial attempts to perform a highly controlled task with regard to the spatial and temporal scales would be more likely to express a true underlying hemispheric specialization than trials run after extensive training.

Using the high- and low-level task categorization, a large body of data regarding hand laterality among nonhuman primates can now be reviewed.

Manual Lateralization for Low-Level Tasks

Manual lateralization in nonhuman primates has been mainly studied by observing simple food reaching in monkeys. Reaching belongs to the minimal manual repertoire of most nonhuman primates (Jolly, 1972) and is developed very early in infancy (e.g., 4 weeks of age in baboons; Fagot, in press). Simple food reaching studies use easily grasped food items that do not necessarily require a precision grip (e.g., hazelnuts, pieces of fruit or pellets; exceptions can be found in Itani, 1957; Vauclair & Fagot, 1987b). Thus, simple reaching obviously falls within the category of tasks that should illustrate low-level tasks. Table 1 indicates that studies of food reaching predominantly show symmetrical distributions of hand biases. The absence of a population level hand bias for low-level tasks is confirmed by observations of several food-oriented, routine manual activities under natural or seminatural conditions (Rawlins, 1986; Rothe, 1973; Schaller, 1963; Vauclair & Fagot, 1987a). Nonasymmetrical distributions were also obtained for holding, pulling, and other gross motor actions (e.g., foraging, Brooker et al., 1981; food holding, Box, 1977; removing an incentive from a horizontal wire and pulling a handle box, Brookshire & Warren, 1962; extracting an object from a vertically oriented clear plastic container, Brookshire & Warren, 1962; picking up an object from an elevated support, Beck & Barton, 1972; moving a block, Beck & Barton, 1972, and Warren & Nonneman, 1976). For these former tasks, significant positive correlations were found between the observed preferences and preferences expressed in the simple reaching task. Such correlations suggest that preferences for low-level tasks such as reaching can be generalized to preferences expressed in other low-level activities.

To supplement our analyses, subject and environment related factors will be examined for food reaching tasks. Table 2 indicates that the strength of hand preference either remains stable or increases with practice. Because practice and age variables are closely linked, results similar to those just given appeared when different age groups were compared with respect to the strength of the preference. Both age and practice variables do not primarily affect the direction of hand preferences (e.g., for the age variable see Brooker et al., 1981; for the practice variable see Lehman, 1980a). Only two studies have found age effects, but they were not consistent (more left-handers were found in adult *Macaca fuscata*, Itani et al., 1963; whereas more right-handers were found in adult *Lemur macaco*, Forsythe & Ward, 1988). By contrast, contextual variables clearly affect the direction of preferences. This is the case for testing conditions, since Deuel & Dunlop (1980) found that 11 of 15 macaques inverted their hand preferences between two testing environments. When food position was examined, it was observed that monkeys primarily reached with the hand closer to the food object (e.g., Cronholm, Grodsky, & Behar, 1963). However, manual preferences (bias and strength) in food-reaching tasks appear to be independent of sex (Brooker et al., 1981; Hamilton, personal communication, 1988)[5] and familial relationship (Brooker et al., 1981).

There is little evidence for simple food reaching demonstrating a specialization of the contralateral hemisphere. For example, when monocular vision was imposed, split-brain monkeys with the optic chiasm cut successfully perform a simple reaching task regardless of which eye, thus hemisphere, was available (Lehman, 1968; Lund, Downer, & Lumley, 1970). These successes show that both hemispheres are able to process the task. A similar conclusion may be derived from Deuel & Dunlop's (1980) study demonstrating that after a unilateral lesion in the association cortex, monkeys used the hand guided by the intact hemisphere, regardless of previous preferences or training. Unilateral lesions of the hemisphere contralateral to the preferred hand did not produce more deficits than did lesions of the ipsilateral hemisphere (e.g., for unilateral lesions of association cortex see Deuel, 1975 and Warren & Nonneman, 1976; for unilateral frontal lesions see Warren, Cornwell, & Warren, 1969). Although several asymmetries in hemispheric performance have been recorded (e.g., Hamilton & Vermeire, 1985; Jason, Cowey, & Weiskrantz, 1984), only the study of Hamilton and Vermeire (1982) has shown significant correlations between a preferred hand and the ability of each hemisphere (left or right) to perform a visual discrimination task. For other studies, the split hemisphere ipsi- or contralateral to the preferred hand did not show any advantage (Hamilton & Vermeire, 1983, 1985).

To sum up, distributions of preferences for food reaching and other routine activities appear to be symmetrical and to some extent dependent on situational contingencies. Because of (a) the paucity of data showing a relation between preferences in low-level tasks and hemispheric specialization, (b) the symmetry of distribution, and (c) contextual effects, one cannot view lateralization for low-level tasks as a common characteristic of a group or population. Rather, we can view it as an idiosyncratic feature and the result of the situational context. The following section is concerned with novel or highly controlled tasks (high-level tasks) with the aim of demonstrating the existence of hemispheric and behavioral laterality at the group level.

Manual Lateralization for High-Level Tasks

Sanford et al. (1984) have tested *Galago senegalensis* with a task requiring an erect posture. Erect posture causes strong

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[5] An article by Ward et al. (1990) mentioned a sex effect in the sense that males, but not females, exhibited a left-hand preference. However, these results remain questionable because they were obtained by summing data gathered on different species.

Table 2

Effects of Several Variables on Manual Preferences in Food Reaching Tasks

Study	Species	N	Strength of preferences	Direction of preferences
		Practice		
Forsythe & Ward (1988)	*Lemur macaco*	33	Stability	Stability
Lehman (1970)	*Macaca mulatta*	24	Stability	Stability
Lehman (1978)	*Macaca mulatta*	171	Increase	Stability
Lehman (1980c)	*Macaca mulatta*	38	Increase	Stability
Warren (1958)	*Macaca mulatta*	17	Increase	?
Lehman (1980b)	*Macaca arctoides*	46	?	Stability[a]
Lehman (1980a)	*Macaca fascicularis*	58	Increase	Stability
		Age		
Forsythe & Ward (1988)	*Lemur macaco*	33	?	More left-handers in young; more right-handers in adults
Box (1977)	*Callitrix jacchus*	58	ns[b]	ns[b]
Brooker, Lehman, Heinbuch, & Kidd (1981)	*Macaca radiata*	69	Increase (r = .33)*	ns
Lehman (1978)	*Macaca mulatta*	171	Increase[c]	?
Fagot, Drea, & Wallen (in press)	*Macaca mulatta*	51	ns	ns
Lehman (1980a)	*Macaca fascicularis*	58	Increase[c]	?
Itani, Tokuda, Furaya, Kano, & Shin (1963)	*Macaca fuscata*	394	?	ns in young; more right-handers in adults
Tokuda (1969)	*Macaca fuscata*	42	ns[b]	ns[b]
Fagot & Vauclair (1988a)	*Gorilla gorilla*	10	ns (r = .07)	ns
		Sex		
Forsythe & Ward (1988)	*Lemur macaco*	33	ns (r = .01)	ns (r = .18)
Brooker et al. (1981)	*Macaca radiata*	69	ns	ns
Lehman (1978)	*Macaca mulatta*	171	ns	ns
Hamilton (personal communication, April 1988)	*Macaca mulatta*	55	ns	ns
Fagot et al. (in press)	*Macaca mulatta*	51	ns	ns
Lehman (1980a)	*Macaca fascicularis*	58	ns	ns
		Filiation		
Forsythe & Wood (1988)	*Lemur macaco*	33	No mother/father–infant significant correlation (r = .19, r = .33)	No mother/father–infant significant correlation (r = .18, r = .33)
Brooker et al. (1981)	*Macaca radiata*	69	No mother–infant significant correlation (r = .08)	No mother–infant significant correlation (r = .17)
		Testing condition		
Warren (1958)	*Macaca mulatta*	15	?	Changes from one condition to the other[d]
		Food condition		
Cronholm, Grodsky, & Behar (1963)	*Macaca mulatta*	15	?	Used the hand nearest to the food
Lehman (1970)	*Macaca mulatta*	24	?	Used the hand nearest to the food
Lehman (1978)	*Macaca mulatta*	171	?	Used the hand nearest to the food
Lehman (1980a)	*Macaca fascicularis*	58	?	Used the hand nearest to the food

[a] Stability despite transient training with the other hand. [b] Computed by Fagot and Vauclair from the data in the original article. [c] Lehman took into account the weight of the monkeys to approximate their age. [d] Preferences are tested either in a primate chair or in a Wisconsin general test apparatus.
* $p < .01$.

spatiotemporal constraints because it requires: (a) dynamic adjustment of the body to counteract gravity (Fortuyn, 1982; Paillard, 1971), and (b) movement regulation of the proximo–distal musculature in reference to the unstable position of the head and body (Miles & Evarts, 1979) and to the location of the goal. For reaching with erect posture, Sanford et al. (1984) reported that 14 out of 25 *Galagos* used their left hand more than 60% of the time; only 5 *Galagos* used the right hand in the same proportion (binomial two-tailed test left vs. right, $p = .10$). Interestingly, when a subgroup of these same subjects was tested for food reaching in a horizontal stance, the biases were more symmetrically distributed (7 left, 5 right: binomial two-tailed test, *ns*). A left-hand preference was recorded in 5 out of 5 black and white ruffed lemurs (*Varecia variegata variegata*) in a situation that involved extreme reaching: Subjects had to lean over an edge to reach for a piece of food floating on water. When tested in a simple reaching task, only one animal of this same group manifested a left-hand preference; the others exhibited no significant preference (Forsythe et al., 1988). Olson, Ellis, and Nadler (1990) provide data on 12 gorillas, 6 gibbons, and 12 orangutans performing a task in which the animals had to maintain a standing posture while retrieving a raisin fixed on a wire mesh above their standing height. All 12 gorillas exhibited a significant hand bias; 10 preferred the right and 2 preferred the left (binomial two-tailed test, $p < .05$). All of the 6 gibbons showed a left-hand bias (binomial two-tailed test, $p < .05$), but no group preference emerged for the orangutans species (4 right and 3 left users, binomial two-tailed test, *ns*). For the gorillas and gibbons, no group preference was observed for a simple reaching task on the floor (for gorillas: right = 5, left = 2, binomial two-tailed test, *ns*; for 8 gibbons including 5 of the 6 animals tested on the mesh retrieval task: right = 2, left = 6, binomial two-tailed test, *ns*).

Other data collected on gorillas (Fagot & Vauclair, 1988a) and baboons (Fagot & Vauclair, 1988b; Vauclair & Fagot, in press) are of interest here. Both gorillas (*Gorilla gorilla*) and baboons (*Papio papio*) were tested with a task of simple reaching for food (10 gorillas and 10 baboons) and with a visuospatial adjustment task requiring the aligning of a window (5 cm × 5 cm) on a Plexiglas panel with an aperture (5 cm × 5 cm) where a hazelnut was located (8 of the 10 aforementioned gorillas and all 10 baboons). In this latter task, precise alignment of the window with the aperture was required for access to the hazelnut (see original articles for further details). The simple food-reaching task produced a symmetrical distribution of the number of left- versus right-handers in both species (for gorillas: right = 3, left = 3, no preference = 4; for baboons: right = 4, left = 6). In the Plexiglas panel task, both gorillas and baboons preferred using their left hand in the adjusting phase (for gorillas: left = 7, right = 1; for baboons, left = 6, right = 0; binomial two-tailed test left vs. right, $p = .07$ and $p = .02$, respectively).

Other evidence for group asymmetry in high-level tasks can be found in the works of Ettlinger and his colleagues. Only their somatosensory studies using tests performed in the dark that required haptic discrimination of geometric forms will be considered here. We will not examine data when vision was involved because in such conditions discrimination was performed visually and the hand had little manipulatory function. In the somatosensory tests, rhesus macaques had to discrimi-

nate and then to push the correct object in order to obtain a reward. The authors found (a) a systematically greater amount of left-hand versus right-hand usage before the training criterion was attained (90% of correct responses out of 200 consecutive trials: Brown & Ettlinger, 1983; Ettlinger, 1961; Ettlinger & Moffet, 1964; Milner, 1969), and (b) a decrease in the left:right ratio (from 1.89 to 1.19) for posttrials, when the training criterion was reached (Ettlinger, 1961; Milner, 1969). These results suggest an advantage of the left hand (right hemisphere) for haptic discrimination, although the differences between the number of left- and right-handers did not reach statistical significance (Ettlinger, 1961: left = 3, right = 0; Ettlinger & Moffet, 1964: left = 7, right = 4, *ns*; Milner, 1969: left = 17, right = 9, $p = .11$; Brown & Ettlinger, 1983: left = 3, right = 1). Pooling together a number of their previous records on the rhesus monkey, Hoerster & Ettlinger (1985) showed that the left-handers needed fewer trials compared to the right-handers to reach the training criterion (210 learning trials on the average for a total of 78 left-handers and 250 learning trials on the average for a total of 77 right-handers; t test, $p = .03$). Altogether, for Ettlinger's studies, the left-hand preference appeared in this task for the first trials, but the right hand became more and more involved in later trials. One can hypothesize that initially the right hand was less able to discriminate than the left hand. However, for postcriterion trials, the left hemisphere's discriminative capacities were sufficient so that the right hand could recognize objects once they became familiar as a result of extended use.

In a study by Fagot et al. (in press), rhesus monkeys had to climb a wire netting and maintain a vertical 3-point posture while they put one hand in an opaque box to discriminate peanuts mixed with sand and stones of different sizes. For a group of 29 subjects, a clear left-hand bias emerged for this tactile discrimination task since 21 rhesus monkeys used preferentially their left hand, 4 preferred their right, and 4 exhibited no preference (binomial two-tailed test left vs. right, $p < .002$). A left-hand bias also appeared when some of the previous subjects were tested with new subjects performing the same tactile task but in a sitting position (left = 22, right = 3: binomial two-tailed test, $p < .001$). In a task in which prehension was spatially constrained by a wire mesh, Fagot et al. (in press) observed a left-hand bias when the animals were in a sitting posture (left = 20, right = 1; binomial two-tailed test, $p < .001$), and when they were in a hanging posture (left = 14, right = 4; binomial two-tailed test, $p = .03$). However, the number of left-handers ($N = 15$) did not significantly exceed the number of right-handers ($N = 12$) for quadrupedal simple reaching on the floor (binomial two-tailed test, *ns*).

Hopkins, Washburn, and Rumbaugh (1989) tested 3 chimpanzees and 2 rhesus monkeys using a task that used the manipulation of a "joystick" that controlled the movement of a cursor on a computer monitor. Subjects had to produce a collision on the screen between the cursor and the target stimulus. Results indicate a significant right-hand preference for all subjects using the joystick (at the group level, binomial two-tailed test 5 vs. 0, $p = .06$), and a significant right hand advantage ($p < .05$ each) in terms of velocity in hitting the target. These five subjects did not express consistent hand preference when tested on reaching into a food well.

Preilowski (1979) used a high-level task to test the manual performances of each hand in *Macaca mulatta*. The monkeys had to produce an isometric pressure of specific duration between the fingertips of the right hand or the left hand. The author experimentally adjusted the difficulty of the task by varying both the spatial and temporal limits defining the grip which had to be maintained. Each monkey ($N = 8$) manifested a greater ability with the right hand than with the left (binomial two-tailed test left vs. right, $p = <.01$). Interestingly, this right hand advantage appeared only at the highest level of difficulty.

Catching implies rapid and precise movements in relation to the trajectory of the moving target. As suggested earlier in this article, this activity must be distinguished from simple reaching, given the spatial and temporal constraints catching encompasses. In one series of studies, the macaques hand preferences in a primate chair were examined while the animals performed a task that involved catching a moving bait (Deuel & Dunlop, 1980; Deuel & Schaffer, 1987).[6] In a first study, 20 rhesus were tested. Results showed 5 right- and 6 left-handers. *Macaca fascicularis* ($N = 25$) were tested later with the same task (Deuel & Schaffer, 1987). Fifteen subjects preferentially used their left and eight preferentially used their right hand (binomial two-tailed test left vs. right, *ns*).

King, Landau, Scott, and Berning (1987) and King, Landau, and Scott (1988) observed squirrel monkeys catching live goldfish: they used predominantly their left hand (left = 11, right = 3, binomial two-tailed test: $p = .06$). In a subsequent experiment involving reaching for stationary food items, these same monkeys along with novel subjects did not express any significant group level hand preference (left = 10, right = 11: King et al., 1988). Data on the catching of food thrown by an experimenter were collected by Kawai (1967). He found a left-hand preference for 9 *Macaca fuscata* and a right-hand preference for 4 when unimanually catching objects in midair (binomial two-tailed test left vs. right, *ns*). Subramoniam (1957) described consistent left-hand usage in 8 *Loris tardigradus* when seizing stationary but live small insects (binomial two-tailed test left vs. right, $p < .01$) and bimanual usage when the prey was large.

To our knowledge, with the exception of the study by Sanford et al. (1984) and Fagot et al. (in press) that revealed no sex difference on manual preferences, there are no data in the literature about sex effects on preference for high-level tasks. Fagot et al. (in press) found in the tactile discrimination task that there were significantly more left-handed adult rhesus monkeys than juveniles. Brinkman (1984, 1987) found a matrilinear related hand preference in a group of *Macaca fascicularis* in a task that involved retrieving a piece of food from a narrow slot using a precision grip. Most of the infants (90 out of 107) displayed the same hand preference as their mother in this precise motor task.

We suggest that preferences in high-level tasks may demonstrate an underlying specialization of the hemisphere contralateral to the used hand. Several arguments tend to support this position. First, fine movements of the hand and fingers seem to be exclusively under the control of the contralateral hemisphere (Brinkman & Kuypers, 1972, 1973; Matsunami & Hamada, 1978). Second, with a finger pressure apparatus, Preilowski (1979; Preilowski, Reger, & Engele, 1986) found no evidence of an immediate intermanual transfer of performance when mon-

keys were forced to use the nonpreferred hand after training with the initially preferred hand. Third, following a unilateral ablation of the second somatosensory (SII) area (combined with bilateral removal of 7b areas or the neocortical commissure) either ipsi- or contralateral to the preoperatively preferred hand, Garcha et al. (1980, 1982) found, with Ettlinger's tactile discrimination task (see above), an impairment in the performance of both hands after lesion of the hemisphere contralateral to the preoperative preferred hand. Removal of the SII area ipsilateral to the preoperatively preferred hand affected neither hand, which is consistent with previous findings by Moffet & Ettlinger (1970). Moreover, inversions of hand choice were observed following ablation in the contralateral group only. A recent study by Hoerster & Ettlinger (1987) partially confirmed this reversal effect.

To sum up, the majority of high-level tasks have produced an asymmetrical distribution of hand biases. It is remarkable that this conclusion applies both to the preference and to the performance asymmetries. Two studies have examined preference and performance asymmetries within the same subjects. In one study (Hopkins et al., 1989), the two measures are in agreement because both indicate an asymmetry in favor of the same hand (i.e., the right). In the second study (Preilowski et al., 1986), the authors found no consistency. Thus, the question remains open as to whether these two measures tap the same phenomenon. Although high-level tasks have led to clear hand preferences, no bias consistency has yet emerged from those tasks. Most of them required different sensory modalities as well as cognitive processes. In humans, it has been shown that sensory (Varney & Benton, 1975) and cognitive components (Nachson & Carmon, 1975) of the task can affect lateral biases; thus, it is not surprising that in the case of nonhuman primates the diversity of tasks used has not led to consistent directional biases.

Conceptual Distinction Between Handedness and Manual Specialization

The previous analyses have shown that nonhuman primates' hand laterality depends on task demands. A two-level classification (low-level vs. high-level) provides a framework to interpret most data. It appears now that the concept of handedness used so far cannot encompass the bidimensionality of hand preferences expressed in high- and low-level tasks.

The importance of the novelty and of the complexity of the task has been raised by Young, Segalowitz, Corter, and Trehub (1983) in a discussion of human laterality in an ontogenetic perspective. These authors have proposed to distinguish the concept of *handedness* from that of *manual specialization*. The former corresponds to lateralized usage on familiar and relatively simple tasks, the latter refers to an asymmetrical hand usage on novel and relatively complex tasks. In addition, for these authors, manual specialization reflects the specialized functions of the hemisphere that better controls the task,

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[6] Given the emotional and the situational constraints a monkey experiences in a primate chair, one can question with MacNeilage et al. (1987) the significance of catching preferences manifested in these studies.

whereas "handedness is not linked to a one to one relationship with cortical dominance" (Young et al., pp. 3–4). Our classification of low- and high-level tasks can partially be integrated into this distinction in the sense that low-level tasks could correspond to handedness and high-level tasks could represent manual specialization. We thus propose to refer to the concepts of handedness and manual specialization to name manual preferences appearing in low- and high-level tasks, respectively. However, our use of these concepts differs from Young et al.'s usage in two ways. First, motor complexity explicitly refers to the spatial and temporal scales of the task. Second, on the basis of the data described above, manual specialization leads to an intersubject bias consistency and handedness is characterized by a lack of population biases of hand preferences.

Relations Between Handedness and Manual Specialization

Because novelty and practice variables are assumed to influence manual laterality, two types of shifts of preference are then expected. First, a given subject can manifest results indicative of either handedness or manual specialization, depending on the nature of administered tasks. Several examples of change in the manual preference as a function of the task have been presented (Sanford et al., 1984; King et al., 1987; Fagot & Vauclair, 1988a, 1988b; Forsythe et al., 1988; Hopkins et al., 1989). Though these findings are recent, their convergence confirms that hand lateralization has to be conceived of as at least a bidimensional phenomenon. Second, a given task can give rise, through practice, to a shift from asymmetrical to symmetrical distribution of hand biases at the group level. Such a shift is exemplified by Ettlinger's (1961) and Milner's (1969) studies. This kind of shift can also be studied in our Plexiglas panel tasks (see above for a presentation of the tasks). For a group of 10 baboons, comparisons were made between individual hand biases for the initial trials (1 to 25) and for the last trials (75 to 100; Vauclair & Fagot, in press). Results have shown that a left-hand preference emerged during the initial 25 trials but disappeared during the last 75 to 100 trials. Parallel comparisons performed for the simple reaching task failed to demonstrate an effect of practice on the distribution of groups preferences for that task. Finally, this shift can be investigated in developmental studies when the weight of novelty–practice factors can be evaluated. Fagot (in press) observed in each of four infant baboons that the first reaching attempts were preferentially realized with the right hand, but that subjects diverged by 4 weeks of age with respect to the side of their preferences. Two of them became ambidextrous and the others fluctuated in their bias. More data are needed to evaluate the generality of this initial right-hand preference.

As a consequence of such individual shifts, changes in the distribution of manual preferences for the group can be expected. An important question is how these changes occur. To us, these shifts are not conceived as systematic, because one could think of situations in which the asymmetry persists despite practice.

In manual specialization, only one hemisphere is supposed to be competent to solve the task. In addition, when fine distal movements are involved, the active hand is necessarily contra-lateral to the specialized hemisphere (Brinkman & Kuypers, 1972). This picture accounts for asymmetrical distributions of manual preferences under the hypothesis that the competent hemisphere is the same for all members of the group under study. To explain the shifts through practice, one must assume that, because of the repetition of the same task (i.e., in handedness), both hemispheres will become competent to solve the task. The neurophysiological mechanisms making the processing of information possible in whichever hemisphere are beyond the scope of this article. Different plausible mechanisms could be proposed such as the access by one hemisphere to an engram localized in the other (e.g., Doty & Overman, 1977), or the formation of bilateral engrams (e.g., Sullivan & Hamilton, 1973). When both hemispheres have become competent to solve the task, hand choice is no more predetermined by a hemispheric asymmetry, thus opening the possibility for other external and individual influences to intervene (e.g., autoreinforcement). Such influences could explain the emergence of individual preferences and also the shape of the population level distribution, which has the best chance to be symmetrical in the absence of strong environmental biases (see, e.g., Cronholm, Grodsky, & Behar, 1963).

Final Comments

The present article argues for a population level asymmetrical hand usage for certain types of tasks. Parallel to these manual asymmetries are several reports of other kinds of asymmetries in nonhuman primates. Neurostructural asymmetries have been found for several taxa in the frontal area of the brain (in apes see, e.g., Holloway & de Lacoste-Lareymondie, 1982; in monkeys see, e.g., Cain & Wada, 1979), in the temporoparietal area (in apes see Lemay & Geschwind, 1975 and Yeni-Komshian & Benson 1976; in monkeys see, e.g., Falk, Cheverud, Vannier, & Conroy, 1986) and the occipital area (in apes see, e.g., Lemay, 1976; in prosimians, see, e.g., de Lacoste, Horwarth, & Woodward, 1988). Other sets of data concern functional asymmetries. In Japanese macaques, a right ear (left hemisphere) advantage has been found to discriminate classes of auditory stimuli (Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978; Beecher, Petersen, Zoloth, & Moody, 1979). Dewson's (1977) and Heffner and Heffner's (1984) results call for a neurological basis in the left hemisphere of this right ear advantage. Other data are related to a neurofunctional superiority of one hemisphere in the processing of visual discrimination tasks. Some studies have found better performances of the left hemisphere (Hamilton, 1983; Hamilton, 1990; Hamilton & Lund, 1970; Hamilton, Tieman, & Farrell, 1974; Hamilton & Vermeire, 1985; Jason, Cowey, & Weiskrantz, 1984), although others have shown right hemisphere advantage (Gazzaniga, 1963; Hamilton & Vermeire, 1988a; Hopkins & Morris, 1989). Hamilton and Vermeire (1985, 1988b) have demonstrated that the side of the advantage was closely dependent on the type of stimuli to be processed. For example, 25 split-brain monkeys exhibited a change from left to right hemispheric superiority when they had to discriminate either lines of different orientations or pictures of monkeys faces.

In sum, the existence of a group bias for manual specialization is convergent with other data on asymmetries, both at the

neurostructural and neurofunctional levels. This convergence of three kinds of asymmetries supports the hypothesis of shared mechanisms and thus, of a possible homology between human and nonhuman primates laterality. Indeed, homology does not prevent dissimilarities (qualitative, e.g., the direction of the asymmetry, as well as quantitative). Many instances of such laterality differences are available in the literature, the most obvious one concerns language and it's neural basis.

Given the preceding analyses, the time is now ripe to enrich our experimental paradigms in the study of nonhuman primates manual lateralization. Human laterality has generally been investigated with highly controlled activities. The same could be done with most nonhuman primate species, given their cognitive and manipulatory abilities (e.g., as expressed in tool use). Investigators of primate hand use should not measure only preferences of simple reaching but propose manual activities that can be a better index of hemispheric specialization.

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Butcher, Geen, Hulse, and Salthouse Appointed New Editors, 1992–1997

The Publications and Communications Board of the American Psychological Association announces the appointments of James N. Butcher, University of Minnesota; Russell G. Geen, University of Missouri; Stewart H. Hulse, Johns Hopkins University; and Timothy Salthouse, Georgia Institute of Technology as editors of *Psychological Assessment: A Journal of Consulting and Clinical Psychology*, the Personality Processes and Individual Differences section of the *Journal of Personality and Social Psychology*, the *Journal of Experimental Psychology: Animal Behavior Processes*, and *Psychology and Aging*, respectively. As of January 1, 1991, manuscripts should be directed as follows:

• For *Psychological Assessment* send manuscripts to James N. Butcher, Department of Psychology, Elliott Hall, University of Minnesota, 75 East River Road, Minneapolis, Minnesota 55455.

• For *JPSP: Personality* send manuscripts to Russell G. Geen, Department of Psychology, University of Missouri, Columbia, Missouri 65211.

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Manuscript submission patterns make the precise date of completion of 1991 volumes uncertain. Current editors will receive and consider manuscripts through December 1990. Should any 1991 volume be completed before that date, manuscripts will be redirected to the newly appointed editor-elect for consideration in the 1992 volume.