

Do Right- and Left-Handed Monkeys Differ on Cognitive Measures?

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Twelve left- and 14 right-handed monkeys were compared on 6 measures of cognitive performance (2 maze-solving tasks, matching-to-sample, delayed matching-to-sample, delayed response using spatial cues, and delayed response using form cues). The dependent variable was trials-to-training criterion for each of the 6 tasks. Significant differences were found between left- and right-handed monkeys on the 2 versions of the delayed response task. Right-handed monkeys reached criterion significantly faster on the form cue version of the task, whereas left-handed monkeys reached criterion significantly faster on delayed response for spatial position ($p < .05$). The results suggest that sensitive hand preference measures of laterality can reveal differences in cognitive performance, which in turn may reflect underlying laterality in functional organization of the nervous system.

Right- and left-handed humans represent distinct neurological populations (Annett, 1985). One example is the relation between handedness and hemispheric specialization in linguistic functions. Approximately 98% of all right-handed individuals exhibit left hemisphere dominance in language functions, whereas 70% of left-handed individuals exhibit left hemisphere dominance for language functions (Rasmussen & Milner, 1977).

Whether handedness predicts or is associated with specific patterns of cognitive function has received some empirical investigation in nonhuman species, but the results have been inconsistent (Lehman, 1993). There have been three general approaches to the study of cognitive functions and handedness in nonhuman primates, including (a) comparisons in performance on certain learning or cognitive measures in relation to hand use, (b) comparison of hand use after lesions to either the contralateral or ipsilateral hemisphere to the preferred hand, or (c) measurement of interhemispheric transfer in learning performance when subjects are forced to use either their left or right hand (Preilowski, 1993; Vauclair & Fagot, 1993b).

For example, Horster and Ettliger (1985) found that left-handed monkeys learned a haptic discrimination task faster than right-handed monkeys. Similarly, Hopkins, Washburn, Berke, and Williams (1992) observed significant task-learning advantages for right- versus left-handed rhesus monkeys. Right-handed monkeys learned two psychomotor tasks significantly faster than left-handed monkeys. However, not all

results have revealed significant or consistent findings. For example, in a series of experiments, Warren (1980) was unable to demonstrate an association between preferred hand use on behavioral measures and specialization in the hemisphere contralateral to the preferred hand. In contrast, Hamilton and Vermeire (1982) reported significant relations between successive visual discrimination performance and use of the dominant hand; however, monkeys that preferred to use either their left or right hand did not differ in learning performance. Thus, right-handed monkeys were no more likely to learn faster than left-handed monkeys, but individual monkeys learned faster when using their dominant hand during training compared with their nondominant hand.

One issue fundamentally related to the assessment of handedness and cognitive functions is whether hand preference represents an endogenous asymmetry in nonhuman primates (Warren, 1980). Restated, the question of considerable debate is whether nonhuman primate hand preferences are an artifact of experiential or environmental, rather than the asymmetric, organization of the nervous system (Corballis, 1992; Ettliger, 1988; Hamilton & Vermeire, 1988a; Warren, 1980). Recent studies clearly suggest that nonhuman primates exhibit population level handedness for different behavioral tasks (e.g., Fagot & Vauclair, 1991; Hopkins & Morris, 1993; MacNeilage, Studdert-Kennedy, & Lindblom, 1987); however, as Ettliger (1988) points out, it is insufficient to simply report hand preferences results; rather, it must be documented that one hand and one hemisphere perform better than another for a particular set of tasks.

In contrast to handedness studies, some investigators have assessed the presence or absence of hemispheric specialization by directly examining performance of the left and/or right hemisphere using split-brain techniques (Hamilton, 1990; Hamilton & Vermeire, 1988b), unilateral lesion approaches (Dewson, 1977; Heffner & Heffner, 1984; Irle, 1990), unilateral presentation of stimuli by way of a divided visual field paradigm (Hopkins & Morris, 1989; Hopkins, Washburn, & Rumbaugh, 1990; Vauclair, Fagot, & Hopkins, 1993), or a dichotic listening paradigm (Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978; Pohl, 1983). In general, all of these approaches have revealed significant findings using a variety of

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different visual and auditory stimuli. From these studies, it appears that hand preference is unrelated to the expression of cognitive asymmetries (Hamilton & Vermeire, 1988a).

To elucidate further the possible relationship between hand preference and performance on a variety of cognitive tasks, we conducted the current study. Two groups of monkeys differing in hand preference for joystick manipulation were compared on six diverse cognitive tasks. Our goal was to determine whether performance varied among groups as a function of hand preference. The particular tasks used in this experiment were selected to provide measures across an array of cognitive dimensions including visual discrimination and memory. Additionally, we previously reported that right-handed monkeys learned two psychomotor tasks faster than left-handed monkeys (Hopkins et al., 1992). In this study, we sought to further determine whether left-handed monkeys exhibit performance deficits limited to particular types of tasks or whether they are manifest of a more general cognitive or learning deficit.

Method

Subjects

The subjects were 12 left- and 14 right-handed rhesus monkeys (*Macaca mulatta*) as measured by hand preference for use of the joystick. Only one of these monkeys was female.¹ Prior to this experiment, all the monkeys had been trained to use a joystick to respond to computer graphic stimuli displayed on a computer monitor (see Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, & Hopkins, 1989; Washburn, in press).

Apparatus

The basic test system that was used to test each monkey has been described elsewhere (Washburn & Rumbaugh, 1992), although the actual units used in the present study were variations on this prototype. Generally, each test system consisted of a personal computer (XT or 386 compatible), a 13-inch color monitor, an analog joystick, and a Gerbrands (No. 5150) pellet dispenser. Fruit-flavored chow pellets were dispensed following each successful trial. For each station, the apparatus was mounted on a cart or shelf and encased in transparent Lexan (hard plastic) for protection, allowing a subject access only to pellets that had been dispensed and to the joystick handle, which protruded through the Lexan toward the subject.

Hand Preferences

The testing and statistical evaluation of hand preference in the subjects of this study have been described elsewhere (Hopkins et al., 1992). Briefly, hand preference for joystick use was assessed in each subject after they had mastered the training tasks for this test system (referred to as *side* and *chase*). On each test station, a joystick was positioned centrally below the bottom edge of the computer screen. For each subject, the hand used to manipulate the joystick was recorded for 200 trials. Hand preference was determined by means of binomial z scores performed on the total number of right-hand responses for each subject relative to the total number of responses. This resulted in both positive (reflecting right-hand preferences) and negative (reflecting left-hand preferences) z score values for each subject. A significance level of $p < .05$ was selected for binomial scores. The monkeys in this study were highly lateralized in their manipulation of the joystick, with no monkey exhibiting less than 80% unilateral hand use (and most manifesting 100% usage for the

preferred hand). There were no ambidextrous monkeys, suggesting that the test system and manipulation demands elicit strong preferences in individual monkeys.

Tasks

The tasks were drawn from the Language Research Center's Computerized Test System battery described in detail elsewhere (Washburn & Rumbaugh, 1992). Generally, each task required subjects to manipulate a joystick to bring a computer-generated cursor (a small white +) into contact with computer graphics stimuli. Manipulation of the joystick resulted in movements of the cursor in an isomorphic direction, unless such movements were prevented by some obstacle (e.g., the border of the screen or a wall of a maze). Unless otherwise noted, stimuli were computer graphic images generated from random characters using stimulus production algorithms described elsewhere (see Washburn, 1990). Correct responses resulted in auditory feedback (a 20-Hz tone) and delivery of pellet rewards. Incorrect responses resulted only in the presentation of a 50-Hz tone. For each task, response time (the interval from the first movement of a cursor until the end of a trial) and response accuracy measures were recorded. Task-specific details for each test are discussed below.

Maze learning (Maze). In the Maze task (see Washburn, 1992), subjects manipulated the joystick so as to move a cursor through a two-dimensional maze on the computer screen, negotiating around computer graphic barriers in order to bring the cursor into contact with small stationary target (a blue square of approximately 1 cm). For the purposes of this study, there were two mazes, one easy (Maze 1) and one difficult (Maze 2). Maze difficulty was judged on the basis of the number of barriers contained within the maze. The actual mazes used in this study were the two training mazes in the study reported by Washburn (1992). The mazes were drawn using graphics software (PC PAINT) and saved as bit-mapped files; each filled the computer screen completely.

On each trial, a predrawn maze template was loaded by the task and presented on the computer monitor. Each trial, the cursor and target were positioned randomly within the maze, which appeared on the screen as a series of white "walls" through which the cursor could not pass. Any white area on the screen (other than the cursor) was interpreted by the task as a wall of the maze. Collision between the cursor and target registered as a correct response, and it resulted in the delivery of a food pellet as well as audio feedback. For each trial, response time (RT) was recorded as the interval between the first joystick movement and collision with the target. Any trial in which the cursor was moved but then remained stationary for 120 s was aborted ("dropped out"), and the trial was readministered. (Thus if a monkey "got stuck and gave up," a new trial would be presented.) A 5-s intertrial interval separated each trial.

Matching to sample (MTS). In the MTS task (Washburn, Hopkins, & Rumbaugh, 1989, 1991), each trial began with the cursor located in the middle of the screen. A target stimulus was presented in a random position on the computer monitor. Subjects were required to direct a collision between the cursor and the sample stimulus (a sampling response) at which time two comparison stimuli appear at random positions on the computer monitor. To respond correctly, subjects were required to move the cursor into contact with the comparison stimulus that matched the sample stimulus. The stimuli consisted of

¹ Male rhesus monkeys are used exclusively for National Aeronautics and Space Administration research on behavior and performance for a variety of physiological and engineering reasons. The one female rhesus in the colony, obtained from a separate source, exhibited a strong right-hand preference and performance advantage, as is consistent with the males from the Georgia State University pool.

planimetric, multicolored stimuli created by software for use with this automated test system (Washburn, 1990). Every 80 trials, eight new stimuli were introduced so as to preclude the effects of proactive interference and enhance generalization in MTS performance.

Delayed matching to sample (DMTS). The DMTS (Washburn et al., 1989) testing format was similar to the MTS paradigm, except that the sample stimulus was erased from the screen prior to the presentation of the comparison stimuli. Additionally, a retention interval was imposed between the sampling response (and subsequent erasure of the sample) and the appearance of the comparison stimuli. The retention intervals were 0, 5, 10, 20 and 40 s randomly selected at each trial. As with the MTS task, every 80 trials, eight new stimuli were presented so as to minimize the effects of proactive interference.

Delayed response task with form cues (DR-Form). The DR-FORM task is a variant on the DMTS paradigm, which was designed to be an automated version of the classic delayed response test procedure (Fobes & King, 1982). At each trial, two different randomly selected stimuli were presented, one in the top left and one in the top right quadrant of the screen. The cursor began each trial at midscreen. Both stimuli remained stationary, but one flashed on and off to indicate that it was the sample for that particular trial. As with the DMTS task, subjects were required to bring the cursor into contact with this flashing sample stimulus; touching the other stimulus was scored as an incorrect response and ended the trial. After the subjects managed touching the sample stimulus, both stimuli were removed from the screen, and the cursor was presented at midscreen throughout a retention interval (0, 5, 10, 20, or 40 s selected randomly each trial). Following this retention interval, the same two comparison stimuli would appear, one in the bottom left and one in the bottom right quadrant of the screen. The position for each stimulus within these quadrants was random, as in the initial phase of the task. Neither stimulus moved nor flashed during this portion of each trial. To respond correctly, the subjects were required to select the stimulus that had originally been flashing. Thus, this task required the subjects to recognize stimuli on the basis of stimulus appearance, despite the presence of the nontarget foil stimulus in both portions of the task.

Delayed response task with spatial cues (DR-Spatial). Conceptually, this task is comparable to previous studies examining spatial memory (Hunter, 1913) and using the delayed response paradigm (Fobes & King, 1982). The task was identical to DR-FORM, except that responding was based on positional rather than form cues. For DR-Spatial testing, one stimulus was randomly selected each trial for presentation. Each trial began with two identical presentations of that stimulus, one in the top left and one in the top right quadrant of the screen. One of the two stimulus positions was identified as the sample by flashing the stimulus that occupied the position. As before, a sampling response was required by having the subjects direct a collision between their cursor and the blinking stimulus. After touching the blinking stimulus, the screen was cleared as in DR-Form for the duration of a retention interval (0 to 40 s). Subsequently, the stimulus was presented in the lower two quadrants of the screen and did not blink. Subjects were required to select the stimulus on the same side of the screen that had been cued in the first portion of the trial (i.e., to contact the bottom left stimulus if the top left stimulus had previously been flashing). Thus, subjects were tested for short-term retention of spatial cues in a task where form cues were irrelevant.

Procedure

Each monkey was trained using a criterion-based protocol on the MTS, DMTS, Maze, DR-Form, and DR-Spatial tasks. This order of task administration was invariant across monkeys, although other tasks unrelated to the present analysis were introduced to the monkeys during intervening sessions. Each subject was tested on a particular task in blocks of 200 trials until performance reached an experimenter-

specified criterion. Criterion was set for the MTS task at 70% accuracy (i.e., training continued on the MTS task until accuracy exceeded 69.9%, at which time the monkey was moved to the DMTS task). The DMTS criterion was 60% over a block of 200 trials (averaged across retention intervals). Subjects were trained on the easy maze of the maze task until response times averaged less than 6 s and subsequently on the harder maze of this task until mean response time was less than 9 s in a block of 200 trials. For the DR-Form and DR-Spatial tasks, training continued until accuracy averaged across retention intervals was in excess of 60%. For each task, the number of trials required to attain criterion were examined as a function of dominant hand use for this sample of monkeys ($\alpha = .01$ throughout).

Results

Some of the dependent measures were correlated (see Table 1). Specifically, the number of trials needed to reach criterion were correlated between the easy and difficult mazes (Maze 1 and Maze 2). Additionally, trials to criterion on the MTS and DMTS tasks, as well as the MTS and DR-Form tasks, were significantly correlated. Because of these significant correlations, some data reduction procedures were subsequently performed. For each subject, the total number of trials needed to reach criterion were averaged (AVG) between the easy and difficult mazes to create one dependent variable referred to as AVG-Maze, reflecting acquisition of the maze tasks. Likewise, for each subject, the number of trials needed to reach criterion on the MTS and DMTS tasks were averaged to create one dependent variable referred to as AVG-MTS.

Multiple analysis of variance (MANOVA) was performed with AVG-Maze, AVG-MTS, DR-Form and DR-Spatial serving as dependent measures and hand preference classification serving as the between-groups variable. Depicted in Table 2 are the average number of trials to criterion as a function of task and hand preference group. As can be seen, there was considerable variability in the number of trials needed to attain criterion for each measure and handedness group. The MANOVA analysis revealed an overall significant effect for hand use, $F(4, 21) = 5.41, p < .005$. Univariate F tests indicated a significant difference in right- and left-handed monkeys for the DR-Spatial memory task, $F(1, 24) = 14.66, p < .01$.

The significant MANOVA warranted further statistical evaluation of the data beyond the univariate F tests provided in the initial analysis. Specifically, we opted to use a step-down analysis of the unique effect of hand use on each dependent

Table 1
Intercorrelations Among Dependent Variables

Variable ^a	1	2	3	4	5	6
1. Maze 1	—					
2. Maze 2	.516**	—				
3. MTS	.019	.341	—			
4. DMTS	.111	.187	.462**	—		
5. DR-Form	-.006	-.081	.446*	-.116	—	
6. DR-Spatial	.109	-.151	.352	.271	.278	—

^aTask descriptions: Maze = maze learning, with Maze 1 rated as easy and Maze 2 as difficult; MTS = matching to sample; DMTS = delayed matching to sample; DR-Form = delayed response with form cues; DR-Spatial = delayed response with spatial cues. * $p < .05$. ** $p < .01$.

Table 2
Average Number of 200 Trial Blocks to Attain Criterion for Left- and Right-Handed Monkeys

Handedness response	Maze 1	Maze 2	MTS	DMTS	DR-Form	DR-Spatial
Left						
<i>M</i>	5.16	8.41	13.60	4.25	8.50	2.16
<i>SD</i>	3.57	4.32	5.08	4.04	4.69	1.14
Right						
<i>M</i>	10.00	9.28	16.40	10.02	6.42	6.07
<i>SD</i>	12.00	8.71	11.80	11.30	5.09	3.67

Note. Values represent the average number of 200 trial blocks to reach criterion. Maze 1 (easy); Maze 2 (difficult); MTS = matching to sample; DMTS = delayed matching to sample; DR-Form = delayed response with form cues; DR-Spatial = delayed response with spatial cues.

measure. Step-down analysis involves the use of analysis of covariance (ANCOVA) with each dependent measure evaluated with respect to the independent variables while having the remaining dependent variables serve as covariates (Tabachnick & Fidell, 1983). The analysis of covariance also allowed for statistical control over variations in task difficulty and order of task presentation within this set of cognitive measures. From this analysis, two significant effects were found. Right-handed monkeys reached criterion on the DR-Form memory task significantly faster than left-handed monkeys, $F(1, 21) = 6.08, p < .03$. In contrast, left-handed monkeys reached criterion significantly faster on the DR-Spatial memory task than right-handed monkeys, $F(1, 21) = 14.83, p < .001$. The weighted means for left- and right-handed monkeys on the DR-Form and DR-Spatial task are shown in Figure 1. No other significant differences were found in performance between left- and right-handed monkeys.

Discussion

Right- and left-handed monkeys differed in performance on delayed-response tasks that required the use of different discriminative cues. Right-handed monkeys performed compa-

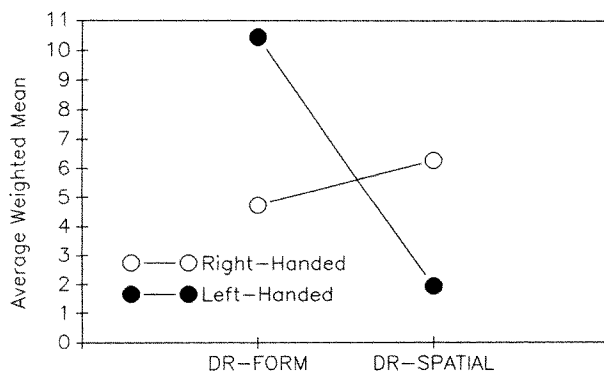


Figure 1. Weighted averages for the number of 200 trial blocks needed to reach criterion for left- and right-handed monkeys on the DR-FORM and DR-SPATIAL tasks. DR-FORM = delayed response with form cues; DR-SPATIAL = delayed response with spatial cues.

rably whether the response was based on spatial or form cues and were significantly more accurate than left-handed monkeys on the latter variant of the task. In contrast, left-handed monkeys were particularly sensitive to spatial cues as a basis for responding. We believe these data represent strong evidence that hand preferences in neurologically intact monkeys can be associated with differential cognitive functioning, a finding supporting our previous results in these monkeys (Hopkins et al., 1992). The data further suggest that such differential cognitive functioning is specific to particular types of functioning and not a general cognitive deficit for either hand-preference population.

Although the findings from this study indicate task specific difference in memory tasks based on hand preference, the results do not unequivocally demonstrate that handedness represents an endogenous asymmetry in these monkeys. For example, it could be argued that hand preferences were accidentally or artificially induced by the joystick training environment and that performance on the DR-Form and DR-Spatial memory tasks were enhanced or inhibited by use of the hand contralateral to the specialized hemisphere. This explanation cannot be fully ruled out based on the results from this study. Notwithstanding, we do not favor this explanation for several reasons. First, as previously noted (Hopkins et al., 1992), altering the joystick testing environment by manipulating the position of the food cup did not result in significant shifts in the distribution of left- and right-handed monkeys. If the joystick testing environment influenced hand preference, then hand preferences should have been more uniform in relation to the position of the food cup. Second, Andrews and Rosenblum (in press) reported that experimentally naive bonnet monkeys (*Macaca radiata*) started out training on the joystick test system with fairly consistent hand preferences for manipulation of the joystick. Finally, in these monkeys, hand preferences were reliable across time, and all subjects were strongly lateralized for use of the joystick. We believe that the significant findings, in our study in comparison to others (Warren, 1980), are based in part on the strength of hand preference assessment implicit in the joystick testing environment.

The data indicating faster spatial learning in left- versus right-handed monkeys are consistent with previous findings of left-hand advantages for performing visual-spatial discriminations or visuomotor tasks by rhesus monkeys (Fagot, Drea, & Wallen, 1991), baboons (Vauclair & Fagot, 1993a), gorillas (Fagot & Vauclair, 1988), and chimpanzees (Hopkins & Morris, 1989; Hopkins et al., 1990), as well as a variety of evidence supporting right-hemisphere specialization of spatial (versus verbal) processing by humans. On the other hand, recent studies on laterality in split-brain (Hamilton & Vermeire, 1988b) and unilaterally lesioned monkeys (Jason, Cowey, & Weiskrantz, 1984) have revealed significant left-hemisphere advantages for visual-spatial discriminations. However, comparing the findings between these studies is difficult because of differences in the stimuli and tasks demands of these studies (i.e., discrimination vs. delayed response with a memory load), as well as in the neurological characteristics of the subject species.

Two other observations are noteworthy. First, some researchers have suggested that behavioral tasks that assess higher

cognitive functions, such as memory or categorization, are better than perceptual or discrimination tasks for revealing differences in hemispheric specialization (Hamilton & Vermeire, 1991; Moscovitch, 1979). From this perspective, perhaps it is not surprising that the only differences found between left- and right-handed monkeys were on two memory tasks. Second, trials to criterion was used as the dependent measure throughout all phases of this study because it allowed for comparison of all tasks on the same scale of measurement. However, criterion was not the same for each behavioral task. For example, a lower criterion (> 60% correct over the course of 200 trials) was used for the memory tasks compared to the learning tasks (Maze and MTS). It could be argued that the use of different criteria unfairly influenced the memory results. However, it is notable that five retention intervals (of 0 to 40 s) were used during the memory tasks, and the 60% correct criterion reflects performance averaged across all five retention intervals. Thus, we consider the 60% correct criterion to be reasonable for the purposes of this study.

An obvious limitation of our study was the near exclusive use of male subjects—dictated for numerous reasons by the colony at hand. Gender differences in functional hemispheric specialization remain a topic of debate in the human literature (McGlone, 1980; Springer & Deutsch, 1989). However, there are documented differences in certain anatomical areas of the brains of male and female rats (Diamond, 1984), and we do not discount the possibility that our effects may be specific to male monkeys.

In conclusion, the results of this study support a growing body of literature indicating hemispheric specialization in nonhuman primates (Ward & Hopkins, 1993). Whether nonhuman functional asymmetries represent analogous or homologous functions to human hemispheric specialization requires further investigation (Corballis, 1989). Notwithstanding, these data suggest that sensitive measures of hand preference may prove useful in explaining differences in learning and cognitive processes both within and between species.

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