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Ward, Jeannette P

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LEFT HAND ADVANTAGE FOR PREY CAPTURE IN THE GALAGO (*GALAGO MOHOLI*)

Jeannette P. Ward

The University of Memphis, USA

ABSTRACT: Efficiency of hand use in nonhuman primates is often difficult to assess because of the relatively small number of responses made with a nonpreferred hand. The present study compared measures of reach efficiency in 8 galagos (*Galago moholi*), 4 left-hand preferent and 4 right-hand preferent subjects, tested in a reach apparatus designed to elicit equal numbers of responses by the left and right hands. The effect of variant or invariant target placement within sessions was also assessed by the use of both blocked and randomized trials. Efficiency was defined in terms of the percentage of successful reaches and the average duration of time required for reach execution. There was no effect of target variance on strength of hand preference or on either measure of performance efficiency. Preferred and nonpreferred hands did not differ with respect to these two measures. There was also no difference in the percentage of successful reaches between the left and right hands. However, for 7 of 8 subjects the left hand generated faster reach times than did the right hand, regardless of hand preference. The greater execution speed with the left arm/hand is interpreted as exemplifying a lateralized neural advantage for the execution of ballistic reaching in galago species. The highly consistent timing of this prey capture behavior in the galago supports the view that this arm/hand movement is ballistic in type.

The search for the evolutionary origins of human laterality has been greatly stimulated by the comparative study of lateralized behaviors in nonhuman primates (Bradshaw & Rogers, 1993; Ward & Hopkins, 1993). Lateral hand preference in simple food reaching has been demonstrated in individuals of many species of prosimian (Ward, 1995) and anthropoid (Kaplan & Rogers, 1994; Hook-Costigan & Rogers, 1996; McGrew & Marchant, 1997; Hopkins, 1996) primates. Hand preference has generally been characterized by the relative frequency of right or left hand use in simple food reaching. However, this measure does not assess possible differences in the performance capacities of the

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Address correspondence to Jeannette P. Ward, Campus Box 526400, Department of Psychology, The University of Memphis, Memphis, TN 38152-6400, U.S.A.

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two hands. Thus, it is often unclear whether a preference for using one hand in a given task is associated with enhanced performance.

When assessment of the performance capabilities of the two hands is undertaken, analyses typically compare the accuracy and/or speed of performance for each hand, thereby providing an indicator of the relative efficiency of each hand. Fragaszy and Mitchell (1990) examined both preference and performance measures of handedness in capuchin monkeys (*Cebus apella*). The preferred hand for performing both unimanual and bimanual tasks was identified and the movement time of the hand performing the task was calculated. This study revealed that, at least for the unimanual task, movement times were significantly faster for the preferred hand. However, conclusions from the results of this study must be somewhat limited by the small number of responses made with the nonpreferred hand. Likewise, in studies of galago reach preference (Larson *et al.*, 1989; Dodson, *et al.*, 1992), direct comparisons of the efficiency of the two hands was also problematic because of the small number of reaches attempted with the nonpreferred hand during testing. When tested in an unrestricted environment in which galagos could freely position themselves in relation to the food, the nonpreferred hand was used in food retrieval less than 20% of the time. Such unequal response samples for the preferred and nonpreferred hands render performance comparisons between the two hands inappropriate.

The galago is a useful model for examining the relative efficiency of preferred and nonpreferred hands, or of the left and right hands, because it has a specialized type of reach that can be timed to provide a measure of efficiency. In the wild, about 80% of the galago's diet consists of insects that are captured by means of a rapid, stereotyped action often referred to as a "smash and grab" movement (Bishop, 1964). It has been suggested that such ballistic capture movements are controlled by a feed-forward or off-line control process that, once initiated, is not modifiable (MacNeilage *et al.*, 1987). In support of this view is our laboratory experience that galagos have never been observed to alter the trajectory of a reach once initiated. We have also observed that when galagos execute a ballistic reach and miss the prey, they often swing the empty, closed hand back to the mouth and even chew once or twice as though the capture had been successful. If the reach used by the galago to retrieve food from a testing apparatus is indeed ballistic in nature, then the amount of time necessary to complete such a reach should be highly consistent from trial to trial. Because the hand with the faster reach time would have an advantage in capturing prey, this behavioral measure provides an ecologically valid

way to compare the performance parameters of the two hands.

The present study evaluated performance in a population of galagos for whom hand preference had been previously established. A testing apparatus was designed to promote the equal use of both hands. The apparatus contained three food cups, one mounted on each of the two side walls and the third placed in the center of the front panel. Perhaps because of the narrowness of the testing apparatus, the galagos did not position themselves directly facing the side food cups. Rather, they executed across-body reaches, using the hand contralateral to the baited cup. Efficiency was evaluated both in terms of the number of successful reaches made by each hand and the amount of time necessary to complete these reaches. Additionally, we examined the possibility that the strength of hand preference for reaching may be influenced by the predictability of the food location. It has been suggested that delivering such rewards in rapid succession, as in a single bout, may induce postural adjustments that bias responding (Marchant & McGrew, 1991). For example, if the same food cup is repeatedly baited, the predictability of the food location may promote the formation of a path habit and an associated reaching posture, thereby artificially inflating the strength of that animal's hand preference. This experiment therefore included sessions in which the placement of the food was varied from trial to trial.

METHODS

Subjects

Subjects were 8 lesser galagos (*Galago moholi*), 5 males and 3 females, averaging 165 g. Four of the animals were wild caught (estimated age at testing > 7 years); the remaining animals were born in the colony at The University of Memphis (mean age at testing 4.5 years). Four male subjects had been determined to be left-hand (LH) preferent and four subjects (one male, Bobby; 3 females, June, Leadtree, and Morgan) to be right-hand (RH) preferent in previous studies (Larson *et al.*, 1989; Dodson *et al.*, 1992). Subjects were housed individually and were maintained on a 12/12 hr light/dark cycle (lights on at 8 pm). Immediately following each daily testing session, the galagos were fed a diet of Purina High Protein Monkey Chow (Ralston-Purina, St. Louis, MO) with mixed fruits and vegetables. All subjects were allowed ad lib access to water. Subjects were treated in accordance with state and federal guidelines.

Apparatus

All experimental sessions were conducted in a clear Plexiglas testing box, shown in Figure 1. A 5-cm diameter food cup was inset 17 cm above the floor on each side wall of the box, as well as the center wall opposite the entrance. A stainless steel carrying cage (10 x 10 x 25.4 cm) served as a start box, which was placed adjacent to the entrance of the testing box.
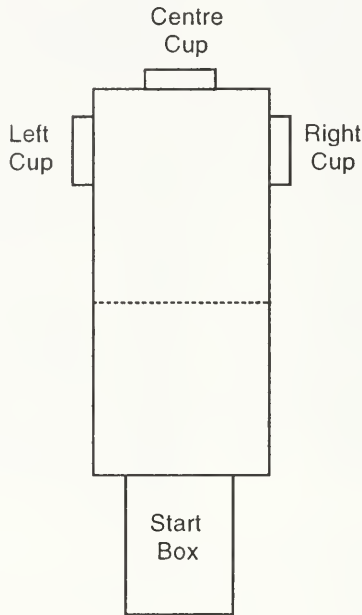

Figure 1. Diagram of the reach apparatus. Three circular clear Plexiglas food cups (2.5 cm in depth) were mounted in the apparatus, one centered in the front wall and one each on the left and right walls positioned 2 cm from the front wall. A 10 cm square opening in the rear wall of the box provided entrance into the testing apparatus. One half of the top panel apparatus was hinged to permit baiting of the food cups.

Procedure

All experimental sessions were videotaped from an overhead view to provide a permanent record for later analysis. A time and date generator indicated elapsed-time (to .01 sec) directly on the videotape. At the start of each trial, the appropriate food cup was baited with a mealworm (*Tenebrio* larvae). The subject was trained to leave the

startbox and approach the food cups to retrieve the mealworm, then to return to the startbox and await the next trial. Thirty completed trials marked the end of each daily session.

Testing Conditions. Each subject completed 8 sessions of 30 trials each for a total of 240 reaches distributed equally across each of the three food cups. Sessions 1-6 comprised the constant locus experimental condition (CON), in which the placement of the mealworm remained constant within each session but varied across sessions. During sessions 1 and 2 the center cup was baited for all animals. Sessions 3 through 6 were counterbalanced so that for 4 subjects (2 LH preferent, 2 RH preferent) the left cup was baited during sessions 3 and 4 and the right cup during sessions 5 and 6. This sequence was then reversed for the remaining 4 subjects. This resulted in a total of 180 trials (60 trials for each food cup) during the CON condition. The final two sessions comprised the variable locus experimental condition (VAR). During each of these sessions, the food cup that was baited was varied from trial to trial according to a pseudorandom schedule so that each cup was baited 10 times, for a total of 30 trials per session. This resulted in a total of 20 trials for each food cup during the VAR condition.

Scoring Categories. The videotapes of each subject's experimental sessions were reviewed to determine the preferred hand for reaching into each of the three cups. For each trial, mealworm retrieval was scored as either right unimanual (R), left unimanual (L), bimanual (B), or mouth (M). Unsuccessful reaches were scored when subjects failed to grasp the mealworm from the cup.

Because the bushbaby's entire body was typically moving forward in conjunction with the forward motion of the arm during the reach, the beginning of the reach could not be defined as the point in which the arm began to move forward. After examining the videotapes of all subjects, a common sequence of movements characteristic of the ballistic reach was identified. As the bushbaby moved toward the foodcup, the hand used to retrieve the mealworm was raised to approximately shoulder height. At this point, the fingers of the hand were closed with the elbow positioned close the body. The elbow then moved abruptly away from the body laterally and the fingers of the hand began to spread apart. The hand then accelerated toward the mealworm with the fingers continually spreading farther apart. Upon contact with the mealworm the fingers closed immediately around it.

The amount of time required to complete each successful reach was determined using a frame-by-frame analysis of the videotaped sessions. The stopwatch on the videotape was used to determine the elapsed time subtended by each successful reach. The beginning of the reach was

defined as the video frame in which the elbow moved laterally away from the body. For each reach, the videotape was advanced to this point and the time on the stopwatch was recorded. The videotape was then advanced to the frame in which the bushbaby's fingers closed around the mealworm. The stopwatch reading from this frame was used to determine the elapsed time between the start and the finish of the reach. All reach time values were determined in hundredths of a second. The videotape was recorded at a speed of 33 frames per second; therefore, the margin of error for determining the start or finish of each reach was calculated to be approximately .03 sec.

To establish how reliably reach times were determined by the observer, 10% of the sessions were randomly chosen and reviewed by a second observer, who independently determined the time required to complete all successful reaches in these sessions. A Pearson correlation revealed a high degree of correspondence between reach times as scored by the two observers ($r = 0.862, p = 0.001$).

RESULTS

Three behavioral measures were used to analyze performance in this task: (1) the strength of the preference for using one hand over the other; (2) the time required for each hand to complete successful reaches; and (3) the reach efficiency of each hand, calculated by dividing the number of successful reaches by the total number of reaches (successful and unsuccessful). The preferred hand for retrieving mealworms from each of the three food cups was determined by the total number of right- and left- hand reaches into each cup.

To determine if the strength of preferred-hand use was affected by the predictability of the food location, the overall percentage of preferred-hand use (% P) during the CON and VAR experimental conditions were compared. No significant difference was found between the two conditions ($M_{CON} = 64.8$, SD = 5.9; $M_{VAR} = 61.3$, SD = 6.42), $t(7) = 1.97$, n.s. The efficiency of hand use in the CON and VAR conditions was also examined. Very few misreaches were made; hence, data from all three food cups were combined to compute an overall reach efficiency percentage for each subject's preferred and nonpreferred hand. No difference was found in the reach efficiency percentages between the CON and VAR conditions for the preferred hand ($M_{CON} = 94.2\%$, $M_{VAR} = 92.1\%$), $t(7) = 1.30$, n. s. However, the reach efficiency of the nonpreferred hand was slightly lower for the CON condition (M = 89.3%) than for the VAR condition (M = 93.1%), $t(7) = 2.47, p < 0.04$.

Finally, reach durations in the CON and VAR conditions were examined. To control for differences in reaching distance, only successful cross-body reaches to the side cups were compared and reaches toward the center cup were not included in this analysis. For each hand, the individual durations for all successful cross-body reaches were combined and the mean reach duration was calculated. These mean reach durations in the CON and VAR conditions were not significantly different from one another for either the preferred hand, $t(7) = 1.95$, n.s., or the nonpreferred hand, $t(7) = 2.30$, n.s. Likewise, no differences between the CON and VAR conditions were found in the mean durations of either right-hand reaches, $t(7) = 2.30$, n.s., or left-hand reaches, $t(7) = 1.92$, n.s.

Because a significant difference between measures for the CON and VAR experimental conditions was found in only one of the five comparisons, data from the two conditions were combined for further analyses. Table 1 provides a list of the percentages of preferred-hand use for each of the three food cups. The design of the testing apparatus resulted in the use of the right hand for the majority of reaches into the left food cup (M = 96.7% of all right-hand reaches) and the use of the left hand for the majority of reaches into the right food cup (M = 94.2% of all left-hand reaches). The hand which subjects preferred to use when reaching into the center food cup was found to be the same hand that had been designated as preferred during previous handedness testing (Dodson, *et al.*, 1992; Larson, *et al.*, 1989). The preferred hand therefore remained constant across these testing periods.

Table 1. Strength of Preferred Hand Use for Reaching into the Left, Center and Right Food Cups. PH = preferred hand classification as right- (R) or left- (L) preferent. %R = percentage of right hand use; %L = percentage of left hand use; %P = percentage of preferred hand use.

Name	PH	Left Cup %R	Center Cup %P	Right Cup %L
Buckwheat	L	93.8	97.5	100
Chewbacca	L	87	83.8	100
Vincent	L	96.3	100	100
Winky	L	100	96.3	100
Bobby	R	98.8	61.3	93.8
June	R	100	93.8	86.3
Leadtree	R	97.5	62.5	83.8
Morgan	R	100	69.7	89.5
Group Mean		96.7	83.1	94.2

The relative efficiencies of the preferred and nonpreferred hands were assessed by comparing the percentages of the total successful reaches with each hand. The overall reach efficiency percentage (RE%) was calculated from reaches into all three cups for both the preferred and nonpreferred hands (see Table 2). Although the RE% for the preferred hand (M = 92.8%) was higher than that of the nonpreferred hand (M = 89.7%), the difference was not statistically significant, $t(7) = 1.41$, n.s. We also calculated the RE% for the left and right hands. As with the preferred/nonpreferred hand analysis, the difference between left and right hands was not significant, $t(7) = 0.08$, n.s.

The movement times of successful cross-body reaches were also compared between hands. For each hand, the individual durations of all successful reaches were combined and averaged. A within-subjects t-comparison of each subject's mean reach times for the preferred and nonpreferred hands revealed no difference between them, $t(7) = 1.00$, n.s. However, the average time required by the left hand (M = 0.1586 sec) to complete a successful reach was significantly less than that required by the right hand (M = 0.1694 sec), $t(7) = 2.74$, $p < 0.029$. As can be seen in Table 3, the left hand advantage in reach time was exhibited by 7 of the 8 galagos.

Table 2. Comparison of Successful Reaches (#S), Misreaches (#M) and Reach Efficiency Percentage (RE%), for the Preferred and Nonpreferred Hands. PH = preferred hand classification as right- (R) or left- (L) preferent.

Name	PH	Preferred Hand			Nonpreferred Hand		
		#S	#M	RE%	#S	#M	RE%
Buckwheat	L	163	21	88.6	77	13	85.6
Chewbacca	L	156	6	96.3	73	0	100
Vincent	L	163	3	98.2	77	12	86.5
Winky	L	157	12	92.9	83	7	92.2
Bobby	R	133	16	89.3	107	29	78.7
June	R	167	1	99.4	73	7	91.3
Leadtree	R	141	14	90.9	99	5	95.2
Morgan	R	134	20	87.0	88	12	88.0
Group Means				92.8			89.7

Table 3. Comparison of the Mean Duration (Sec) of the Ballistic Reaches with the Left and Right Hands. N = number of reaches used in computing the mean speed.

Name	Left Hand			Right Hand		
	Mean	SD	N	Mean	SD	N
Buckwheat	.1114	.0270	80	.1219	.0270	75
Chewbacca	.1903	.0742	80	.1963	.0605	60
Vincent	.1791	.0390	80	.2034	.0513	77
Winky	.1290	.0280	80	.1536	.0451	80
Bobby	.1141	.0269	75	.1199	.0279	79
June	.1645	.0208	69	.1684	.0228	80
Leadtree	.1760	.0266	67	.1959	.0377	78
Morgan	.2038	.0245	68	.1961	.0255	80
Group Mean	.1586	.0357		.1694	.0343	

DISCUSSION

The apparatus employed in this study was highly successful in providing equivalent samples of left and right hand use and thereby permitted comparison of the efficiency of hand use in terms of lateral preference. The results suggest that hand preference, per se, is not a factor in the efficiency of this type of ballistic prey capture; neither reach duration nor prey capture was enhanced as a function of lateral preference. The left hand, however, did require significantly less time to complete a reach than did the right hand across our sample of subjects. The durations of left-hand reaches were shorter in seven of the eight animals tested, four of which were left-preferent and three of which were right-preferent.

The results of this study show that the movement time of the ballistic reach is relatively invariant in the right and left hands of a given individual. Although this suggests a feed-forward type of motor response that might be expected to be hard-wired in the nervous system, it is possible that experiential factors may influence speed of movement. For example, the one galago, Morgan, who demonstrated a slightly faster right-hand movement time, had, prior to inclusion in the present study, undergone extensive testing in a visuospatial reach task in which she used the right hand almost exclusively. This task required the animal to retrieve a food reward from a moving turntable, the speed of which was gradually increased to determine the asymptotic level of

performance. This intensive right-hand practice may explain Morgan's faster right-hand performance relative to the other subjects. It is possible that in this case an endogenously lateralized characteristic was modified by experience. A study of lateralized foraging patterns in the gentle lemur (*Hapalemur griseus*) found that those patterns which were most commonly used were executed more quickly (Butler *et al.*, 1995), a response time advantage which was perhaps the result of rehearsal of specific patterns of feeding.

The left hand superiority in movement time does seem to constitute a lateral advantage for the execution of movements that require quick response. It has been shown in cats that reach durations are shorter for the preferred paw than for the nonpreferred paw (Fabre-Thorpe *et al.*, 1993). Furthermore, cats that are lateralized in this action tend to prefer their left paws and have shorter movement times than cats that do not exhibit lateralized reaching behavior. Such laterality may thus have adaptive value, as quicker reaches for prey may enhance success in predation. Humans have also been shown to produce ballistic responses faster with their left hands (Guiard *et al.*, 1983; Azemar *et al.*, 1990). A left side advantage in ballistic movements may therefore prove to be a conservative evolutionary trait. These results are also supportive of the theory of MacNeilage *et al.* (1987) that proposes an endogenous superiority for visually-guided reaching by the left hand in prosimians.

The ballistic character of the galago reach, first suggested by Bishop (1964), is confirmed in this study by the response time invariance. Although there was some variability in the average movement time between subjects (ranging from a low of 0.1167 sec to a high of 0.1999 sec), the standard deviations for left- and right-hand mean durations for each subject shown in Table 2 confirm that the individual mean durations were remarkably uniform. In fact, the average standard deviation for both left-hand (.0357 sec) and right-hand (.0343 sec) reaches approximated the estimated margin of error (.03 sec) for determining the start or finish of each reach from the videotape still-frame (see Methods section). The findings therefore support the contention that these movements are quite invariant in their timing as would be expected for a feed-forward ballistic system.

Although only one species was examined in this study, I propose that this left-hand functional specialization for feed-forward rapid reaching movements may be characteristic of all galago species. Reach efficiencies were also determined for one left-preferent *Galago senegalensis braccatus*, a larger species of galago. This galago was the only one of its species available to us and was old and in failing health. Reach durations for this animal, Weisel, were substantially greater than

the mean reach durations for the *G. moholi*. However, it is important to note that data from this animal were consistent with the data from *G. moholi* with regard to the direction of lateral advantage. Weisel's mean reach duration was shorter for the left hand (M = 0.3002, SD = 0.1244) than for the right (M = 0.3285, SD = 0.0843). Thus, although species differences in absolute reach durations may exist, this result suggests that a left-hand superiority for movement time may be found across galago species.

To this point in the discussion, behavioral advantage in prey capture has been couched solely in terms of the greater speed of the left hand in execution of the ballistic reach. It might be asked: if left specialization has adaptive significance for feeding, why in this study was no difference found between the left and right hands in successful prey capture. The answer seems to be that the requirements of the capture task did not adequately challenge the ballistic reach. A large part of the diet of galagos in their natural habitat is composed of insects, especially flying insects. The advantage of the ballistic reach must be inherent in the rapid movement of the natural prey species. The slowly undulating mealworms placed in the cups of the test apparatus were essentially static targets that rarely resulted in reach errors. Thus, the question of greater left hand efficiency in successful capture must await a different test method, one that challenges the speed of the ballistic reach with the speed of the target.

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