

RESEARCH ARTICLE

Laterality in Semi-Free-Ranging Black and White Ruffed Lemurs (*Varecia variegata variegata*): Head-Tilt Correlates With Hand Use During Feeding

ELIZA L. NELSON^{1,2*}, JAIME M. O'KARMA¹, FELICIA S. RUPERTI², AND MELINDA A. NOVAK¹

¹Department of Psychology, University of Massachusetts, Amherst, Massachusetts

²Monkeyland Primate Sanctuary, Plettenberg Bay, Western Cape, South Africa

Previous studies in human and chimpanzee infants have identified a predictive relationship between early rightward head orientation and later right hand use. Data from lemurs suggest a leftward bias in hand preference, but there are no data on head positioning. The purpose of this study was to examine the relationship between head and hand preferences in the black and white ruffed lemur (*Varecia variegata variegata*). Ruffed lemurs rotate the head vertically during chewing in a behavior called head-tilting. Frequency of head-tilting and bouts of unimanual hand use were measured during normal feeding in a semi-free-ranging population of lemurs. Subjects were provisioned at feeding platforms twice daily with fresh fruits, vegetables, and other food items. Sampling was spontaneous and all observations were videotaped. No group-level bias was found for head-tilting, but a left hand bias emerged for hand use. A positive relationship was found between direction of head-tilting preference and direction of hand use preference such that left head-tilts increased as left hand use increased. Furthermore, left head-tilts increased as the degree of hand preference lateralization increased. When the hand used to bring food to the mouth just before head-tilting was examined, there was a strong bias for the left hand to precede left head-tilts. For right head-tilts, however, lemurs were equally likely to use either hand before head-tilting. Overall a strong relationship was found between the left hand and left head-tilting in black and white ruffed lemurs, suggesting a common link between these behaviors. However, the direction of bias was different from that seen in human and chimpanzee studies. Additional studies on patterns of laterality would be informative for understanding how laterality has changed across the primate order and the adaptive significance of laterality in primates. *Am. J. Primatol.* 71:1032–1040, 2009. © 2009 Wiley-Liss, Inc.

Key words: black and white ruffed lemur; prosimian; laterality; head preference; hand preference

INTRODUCTION

Studies of laterality in primates have largely focused on hand use. The majority of humans are indisputably right handed [Annett, 2002]. In contrast, a recent meta-analysis of nonhuman primate hand use by Papademetriou et al. [2005] reported a population-level left hand bias for lemurs, some of the oldest extant primates. The marked difference between humans and lemurs is striking. Studies of lemur laterality are therefore important not only to elucidate the origins of handedness in primates, but also to understand how hand use has changed across the primate order [Watson & Hanbury, 2007]. Moreover, examining the relationships between hand use and other lateral biases will provide insight into the underlying mechanisms of laterality and how lateral biases might interact [Cantalupo & Ward, 2000; Ward & Cantalupo, 1997].

Of particular interest is the relationship between head positioning and hand preference. Previous studies in human (*Homo sapiens*) and chimpanzee (*Pan troglodytes*) infants have identified a predictive relationship between early rightward head orientation and later right hand use [Hopkins & Bard, 2000; Michel, 1981]. Head orientation was measured experimentally in human infants while they were in a supine position. The infant's head was first held in a fixed position and then released, and

*Correspondence to: Eliza L. Nelson, Department of Psychology, University of Massachusetts, Tobin Hall, 135 Hicks Way, Amherst, MA 01003. E-mail: enelson@cns.umass.edu

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subsequent head positioning was observed. Hand preference was quantified by examining toy-reaching behavior. Group right biases were found for head orientation and hand preference. Furthermore, head orientation preference measured from 3–8 weeks of age predicted hand preference at 16 and 22 weeks [Michel, 1981]. Similar findings were obtained for chimpanzees. Group right biases were found for head orientation (obtained from the sleeping position of nursery-reared chimpanzees) and hand preference (obtained from performance on the TUBE task). The TUBE task measures coordinated bimanual action [see Hopkins, 1995]. In addition, neonatal supine head orientation preference predicted juvenile hand preference on the TUBE task [Hopkins & Bard, 2000].

In contrast to these findings in human and chimpanzee infants, Westergaard et al. [1998] reported a leftward head orientation preference and a negative correlation between head orientation and later hand use in infant capuchin monkeys (*Cebus apella*). Infant head position was observed as the infant rode dorsally on its mother's back when it was 1–2 weeks of age. Hand preference was measured from object manipulation at 23–24 weeks of age and again at 47–48 weeks of age. Head preference was negatively correlated to the early assessment of hand preference and there was no relationship between head preference and the later assessment of hand preference. However, the observations of head orientation were taken when the infant was in a prone position, not supine as in the human and chimpanzee studies. There have been no studies on head positioning and hand use in prosimians.

The goal of this study was to examine the relationship between head and hand preferences in the black and white ruffed lemur (*Varecia variegata variegata*). Data were collected on head-tilting and hand use during normal feeding. Head-tilting is a behavior that aids in food processing. Once food is in the mouth, lemurs sometimes rotate their heads vertically to chew (Fig. 1). It has been suggested that this positioning of the head allows the food to be kept between the premolar and molar teeth [Britt, 2000; Pereira et al., 1988]. Head-tilting seems to be a trademark of all ruffed lemurs. Head-tilting during feeding has been noted in both captive [Pereira et al., 1988] and wild [Britt, 2000] black and white ruffed lemurs as well as captive red ruffed lemurs (*V. variegata rubra*) [Zehr, personal communication]. Head-tilting may be related to preferred bite size and diet. In a study on gape size, red ruffed lemurs were found to eat significantly larger sized food items than Coquerel's sifakas (*Propithecus coquereli*) [Harstone-Rose & Perry, 2007]. Ruffed lemurs are fruit eaters, whereas sifakas are leaf eaters. The specialized fruit diet coupled with the fact that most prosimian species engage in less manipulative activities during feeding compared with other primates may have led



Fig. 1. *Varecia* right head-tilt.

to the large preferred bite size and head-tilting behavior in ruffed lemurs.

Head-tilting is physically distinct from other head positions such as head turning or head-cocking (Fig. 2). A head turn is a rotation in the horizontal plane and a head-cock is a rotation about the rostrocaudal axis [Rogers et al., 1993]. Black and white ruffed lemurs have been noted to head-cock in response to visual and auditory stimuli [Menzel, 1980]. Feeding was the only context that elicited head-tilting for the lemurs observed in this study. Head-tilting occurred after both oral and manual food retrievals. To the best of our knowledge, this is the first examination of lateral biases in head-tilting behavior.

Previous work on hand preference in black and white ruffed lemurs is limited to a single study by Forsythe et al. [1988], which found a left hand bias in a small sample ($n = 5$) of lemurs when posture was challenged. An important contribution of this study was to replicate and extend those findings in a larger sample ($n = 21$) of lemurs. Another major contribution of this work was to examine the link between hand use and head positioning in lemurs for the first time. Although this study was not developmental in nature, we tested the hypothesis that head-tilting predicts hand preference in black and white ruffed lemurs. Ruffed lemurs have a short gestation of 102 days, which means that infants are fairly underdeveloped at birth. Infants are transported by mouth by the mother rather than clinging to her ventral (e.g. *Macaca mulatta*) or dorsal (e.g. *C. apella*) surface like some other primates [Vasey, 2003]. However, infants have been observed to grip the



Fig. 2. Head positions in *Varecia*. Left to right: head forward, left head turn, left head-cock, left head-tilt.

TABLE I. Individual Head-Tilt Data by Age

Subject	Age	Age class	N	HTI	P
Galdikas	2	Young adult	2	DD	DD
Fossey	3	Young adult	6	DD	DD
Leakey	3	Young adult	14	-0.29	Ambi-preferent
Hiawatha	4	Young adult	1	DD	DD
Maya	4	Young adult	39	0.38	Significantly right
Shakespeare	4	Young adult	23	0.57	Significantly right
Madiba	5	Young adult	45	-0.10	Ambi-preferent
Madonna	5	Young adult	52	-0.23	Ambi-preferent
Mozart	5	Young adult	1	DD	DD
Oprah	5	Young adult	26	-0.46	Significantly left
Othello	5	Young adult	45	0.07	Ambi-preferent
Ozzy	5	Young adult	81	-0.04	Ambi-preferent
Fenway	7	Adult	11	0.45	Ambi-preferent
Darwin	7	Adult	5	DD	DD
Leonardo	7	Adult	6	DD	DD
Beethoven	8	Adult	13	-0.60	Significantly left
Venus	8	Adult	19	-0.40	Ambi-preferent
Rasputin	14	Adult	23	-0.13	Ambi-preferent
Nostradamus	15	Adult	9	DD	DD
Einstein	17	Adult	24	0.17	Ambi-preferent
Rupree	19	Adult	12	0.00	Ambi-preferent

Age class, Young adult = 2–6 years of age, Adult = 7 years of age and older; N, number of directional (left or right) head tilts; HTI, Head-Tilt Index as calculated by the formula $(R-L)/(R+L)$ with a minimum of 10 head-tilts; P, preference as calculated by Binomial test $P < 0.05$; DD, data deficient.

mother's fur during nursing [Kress et al., 1978]. Because lemurs first feed with their mouths as infants and are born with limited manual ability, we hypothesized that head positioning preferences may be established before hand use preferences. Therefore, an early bias in head positioning may predispose, but not necessarily cause, a later bias in hand use within an individual if a common mechanism underlies both behaviors.

METHODS

Study Site and Subjects

Data were collected at Monkeyland Primate Sanctuary in Plettenberg Bay, Western Cape, South Africa. The sanctuary is funded by eco-tourism and open daily to the public for guided walking safaris. Monkeyland houses ten semi-free-ranging primate species including the study species, the black and white ruffed lemur. The other species are the black lemur (*Eulemur macaco*), ringtailed lemur (*Lemur catta*), white-handed gibbon (*Hylobates lar*), tufted or brown capuchin (*C. apella*), brown howler monkey

(*Alouatta fusca*), spectacled langur (*Trachypithecus obscurus*), black-handed spider monkey (*Ateles geoffroyi*), common squirrel monkey (*Saimiri sciureus*), and vervet monkey (*Chlorocebus aethiops*).

Observations were made on 21 black and white ruffed lemurs. Lemurs were individually identified by differences in pelage, face, and tail characteristics [Nelson & Ruperti, 2006]. Lemurs ranged in age from 2 to 19 years old ($M = 7.63$ years, $SD = 4.91$ years, see Table I). 17 of the lemurs were born at the sanctuary, 3 lemurs came from zoos in South Africa, and 1 lemur had been a pet and was voluntarily surrendered by the owner. The majority of the lemurs ($n = 19$) were housed outdoors on a 12 ha ($120,000 \text{ m}^2$) plot of indigenous afro-temperate forest. The remaining subjects ($n = 2$) were housed on a separate outdoor forest plot $2,500 \text{ m}^2$ in size because of age and previous injuries not affecting their participation in this study. Electrified fencing surrounded both enclosures. All subjects were provisioned twice daily at feeding platforms with fresh fruits, vegetables, and other foods. Common food items included apples, oranges, broccoli, and sweet

potato. There were 12 feeding platforms in the large enclosure and 1 feeding platform in the smaller enclosure. Water was provided at drinking stations throughout the enclosures. Animals also drank from ponds and places where the water collects naturally.

Procedure

Lemurs were videotaped during normal feeding by three independent observers from July to August 2006 and May to June 2007. All observations occurred between 0730 and 1730 hr. The observer stood at least 1 m away from the feeding station during filming. An observation began when a lemur was seen at a feeding platform and ended when the lemur stopped eating or left the platform. Lemurs were identified by name on the videotape and the primary investigator confirmed all identifications. A total of 213 observations were filmed. Of these, 7 observations were excluded from the data analysis because the lemur's identity could not be verified from the videotape. Monkeyland Primate Sanctuary granted permission for this study. The research was also approved by the University of Massachusetts Amherst Institutional Animal Care and Use Committee (IACUC) and complied with animal welfare laws in South Africa.

Black and white ruffed lemurs pick up food with both the mouth (oral feeding) and the hands (manual feeding). The number of observations for each lemur varied. Therefore, feeding was measured in bouts as opposed to frequency to maintain independence in data points and to avoid inflating individual preferences. Bouts of oral feeding began when a food item was picked up with the mouth and ended when the lemur finished picking up food with the mouth or changed to feeding with the hands. Bouts of hand use began when the food item was manipulated (either picked up from the feeding platform or moved from the mouth to the hand) and ended when the lemur finished eating the food item, dropped the food item, or changed hands. No lemur picked up or manipulated food bimanually, so analyses of hand use only addressed unimanual actions. Head-tilting was operationally defined as an upward rotation of the head in the vertical plane of at least 45° with a duration of at least 2 s. Head-tilts were measured in frequency as independent events and were scored as midline, left, or right.

Data Analysis

Data from the first and second sampling periods (2006 and 2007) were combined to increase power for statistical tests. Lemurs that did not have a minimum of ten directional (left or right) head-tilts or ten bouts of hand use were excluded from preference analyses. According to this criterion, 14 lemurs had sufficient data for head-tilt and hand use analyses. An additional five lemurs had data for hand use

analyses only. Preferences were characterized at the group level along a continuum of -1.00 (Left) to 1.00 (Right) using the following measures. A Head-Tilt Index (HTI) was calculated by subtracting the number of left head-tilts from the number of right head-tilts and then dividing by the total number of left and right head-tilts ($HTI = \text{Right} - \text{Left} / \text{Right} + \text{Left}$). A Handedness Index (HI) was calculated by subtracting the number of left hand responses from the number of right hand responses and then dividing by the total number of hand responses ($HI = \text{Right} - \text{Left} / \text{Right} + \text{Left}$). The number of head-tilts and hand use bouts varied by lemur. HTI and HI scores were correlated with the total number of head and hand responses using two-tailed Pearson correlations to determine whether sampling methods biased preference scores [Hopkins, 1999]. The absolute value of HTI (ABS-HTI) and HI (ABS-HI) scores was computed to assess the strength of head-tilt and hand use preferences.

One-sample *t*-tests were performed on HTI and HI scores (test value = 0) to test for population-level biases. Head and hand preferences were characterized at the individual level using two-tailed Binomial tests. Subjects were then classified as always left, significantly left, ambi-preferent, significantly right, or always right based on the model given by McGrew and Marchant [1997]. χ^2 goodness-of-fit tests were performed using exact probabilities [Radlow & Alf, 1975] to assess whether head and hand preference distributions differed from an unbiased hypothetical distribution of 25% left preferent, 50% ambi-preferent or mixed preferent, and 25% right preferent as defined by Annett [2006].

Effects of age on strength and direction of head-tilt and hand use preferences were examined using two-tailed Pearson correlations. Lemurs were further divided into young adult and adult groups. Young adults were lemurs between 2 and 6 years of age and adults were lemurs 7 years of age or older. One-way analysis of variance tests were conducted using HTI, ABS-HTI, HI, and ABS-HI as dependent variables and age group as the independent variable to test for differences in head and hand preferences in younger versus older lemurs.

A 3×3 χ^2 analysis was performed to determine whether there was a relationship between head-tilt position (midline, left, or right) and food entry preceding head-tilt (oral pick up, left hand, or right hand). Because the majority of head-tilts were observed after manual food entries, χ^2 goodness-of-fit tests corrected for continuity were used to examine whether one hand preferentially preceded each head-tilt position. The relationship between head-tilt and hand use was further examined with linear regression analyses. HI scores were regressed onto HTI scores to test the hypothesis that head-tilting predicts hand use in black and white ruffed lemurs. ABS-HI scores were regressed onto ABS-HTI

scores to determine whether head-tilting preference strength predicts hand use preference strength. ABS-HI scores were also regressed onto HTI scores to determine whether direction of head-tilting preference predicts hand preference strength. Finally, HI scores were regressed onto ABS-HTI scores to determine whether the strength of head-tilting preference predicts the direction of hand preference. α was 0.05 for all statistical tests.

RESULTS

Head-Tilting

Head-tilts were largely executed while the lemur was seated compared with other postures (sitting = 526, quadrupedal standing = 99, vertical clinging = 13, other = 5). In total, 643 head-tilts were observed. Of these, 181 were midline head-tilts, 241 were left head-tilts, and 221 were right head-tilts. Head-tilt preferences were based on directional head-tilts only. Individual data are given in Table I. HTI scores ranged from -0.60 to 0.57 ($M = -0.04$, $SD = 0.35$). HTI scores were not correlated with the number of head-tilts observed for each lemur ($r = 0.017$, $P > 0.05$). A one-sample t -test did not find a bias for head-tilting at the group level, $t(13) = -0.468$, $P > 0.05$. Binomial tests revealed that four lemurs were lateralized for head-tilting at the individual level. Using the classification system of always left, significantly left, ambi-preferent, significantly right, and always right, no lemur was always left, two lemurs were classified as significantly left, ten lemurs were ambi-preferent, two lemurs were significantly right, and no lemur was always right for head-tilting (Table I). This distribution of head-tilt preferences did not differ from an unbiased distribution, $\chi^2 = 2.571$, $df = 2$, $P > 0.05$. Strength of head-tilt preferences as calculated by ABS-HTI scores ranged from 0.00 to 0.60 ($M = 0.28$, $SD = 0.20$). There was no relationship between age and direction of head-tilting preference (HTI, $r = 0.004$, $P > 0.05$) or strength of head-tilting preference (ABS-HTI, $r = -0.394$, $P > 0.05$). There was also no effect of age group on direction of head-tilt preference, $F(1,13) = 0.139$, $P > 0.05$, or strength of head-tilt preference, $F(1,13) = 0.046$, $P > 0.05$.

Hand Use

Individual hand use data are given in Table II. In total, 1104 bouts of unimanual hand use were observed. Lemurs spent more time in manual feeding compared with oral feeding. Time spent feeding with the hands as a percentage of total feeding bouts ranged across individuals from 42% to 91% ($M = 74\%$). HI scores ranged from -1.00 to 0.47 ($M = -0.35$, $SD = 0.47$). HI scores were not correlated with the number of hand use bouts calculated for each lemur ($r = 0.186$, $P > 0.05$).

A one-sample t -test revealed a significant group-level left bias, $t(18) = -3.257$, $P < 0.01$. The average percentage of left hand use across lemurs with sufficient observations was 67% ($n = 19$). Strength of hand use preferences as calculated by ABS-HI scores ranged from 0.07 to 1.00 ($M = 0.47$, $SD = 0.34$). Binomial tests revealed that 11 lemurs were lateralized for hand use at the individual level. According to the five-group classification system, three lemurs were always left, seven lemurs were significantly left, eight lemurs were ambi-preferent, one lemur was significantly right, and no lemur was always right (Table II). This distribution of hand use preferences differed from an unbiased distribution, $\chi^2 = 9.000$, $df = 2$, $P < 0.05$. There was no relationship between age and the direction of hand use preference (HI, $r = -0.011$, $P > 0.05$) or the strength of hand use preference (ABS-HI, $r = -0.007$, $P > 0.05$). There was also no effect of age group on direction of hand use preference, $F(1,18) = 0.017$, $P > 0.05$, or strength of hand use preference, $F(1,18) = 0.287$, $P > 0.05$.

The Relationship Between Head-Tilting and Hand Use

The manner in which food entered the mouth before each head-tilt was examined. Midline head-tilts were preceded by 13 oral, 107 left hand, and 55 right hand food retrievals. Left head-tilts were preceded by 28 oral, 173 left hand, and 31 right hand food retrievals. Right head-tilts were preceded by 14 oral, 106 left hand, and 97 right hand food

TABLE II. Individual Hand Use Data

Subject	N	%L	HI	P
Beethoven	13	100	-1.00	Always left
Nostradamus	13	100	-1.00	Always left
Oprah	55	100	-1.00	Always left
Rasputin	44	91	-0.82	Significantly left
Leakey	25	88	-0.76	Significantly left
Venus	50	84	-0.68	Significantly left
Madonna	147	82	-0.65	significantly left
Fenway	57	68	-0.37	Significantly left
Madiba	98	65	-0.31	Significantly left
Othello	126	63	-0.27	Significantly left
Galdikas	11	82	-0.64	Ambi-preferent
Shakespeare	58	55	-0.10	Ambi-preferent
Maya	63	54	-0.08	Ambi-preferent
Rupee	15	53	-0.07	Ambi-preferent
Darwin	30	47	0.07	Ambi-preferent
Einstein	48	44	0.13	Ambi-preferent
Mozart	23	39	0.22	Ambi-preferent
Leonardo	15	27	0.47	Ambi-preferent
Ozzy	205	38	0.24	Significantly right
Fossey	5	100	DD	DD
Hiawatha	3	67	DD	DD

N, number of hand use bouts; %L, percent of left hand use; HI, Handedness Index as calculated by the formula $(R-L)/(R+L)$ with a minimum of 10 hand use bouts; P, preference as calculated by Binomial test $P < 0.05$; DD, data deficient.

retrievals. This distribution of head-tilt positions and food entry methods was significantly different from chance, $\chi^2 = 54.5$, $df = 4$, $P < 0.01$. Further examination focused on differences between left and right hand food entries for each head position (Fig. 3). There were significantly more left hand food entries than right hand food entries for midline head-tilts, $\chi^2 = 16.06$, $df = 1$, $P < 0.001$. Similarly, there were also more left hand food entries before left head-tilts than right hand food entries, $\chi^2 = 97.46$, $df = 1$, $P < 0.001$. There was no difference between left and right hand food entries for right head-tilts, $\chi^2 = 0.32$, $df = 1$, $P > 0.05$.

A linear regression analysis found that direction of head-tilt preference predicted direction of hand preference, $F(1,12) = 12.659$, $P < 0.01$ (Fig. 4, Left panel). A positive correlation between head-tilt and hand use was found such that left hand use increased as left head-tilts increased ($r = 0.716$, $P < 0.01$). Direction of head-tilt preference also predicted

strength of hand preference, $F(1,12) = 24.104$, $P < 0.01$ (Fig. 4, Right panel). Hand preference strength increased as left head-tilts increased, meaning that strongly lateralized lemurs made more left head-tilts compared with weakly lateralized lemurs ($r = -0.817$, $P < 0.01$). There was no relationship between strength of head-tilt preference and strength of hand use preference, $F(1,12) = 2.069$, $P > 0.05$, or strength of head-tilt preference and direction of hand preference, $F(1,12) = 3.134$, $P > 0.05$.

DISCUSSION

Semi-free-ranging black and white ruffed lemurs exhibited a left hand preference during feeding that was related to head-tilting, a vertical head positioning behavior that may help process food. A left hand bias has also been found in other prosimian species such as black lemurs [*L. macaco*; Forsythe & Ward, 1988], bushbabies [*Galago senegalensis*; Sanford et al., 1984], and ringtailed lemurs [*L. catta*; Milliken et al., 1989]. Forsythe et al. [1988] previously reported a left hand bias in black and white ruffed lemurs ($n = 5$) as measured by three different feeding tasks. In the first task, lemurs were observed foraging for grass, leaves, twigs, and sticks. In the second and third tasks, orange wedges and banana slices were thrown into different parts of the enclosure and lemurs were required to navigate to and retrieve the items. Under the observational foraging condition, the average percentage of left hand use was only 56%, whereas the experimental conditions elicited percentages of 96 and 100%. The authors attributed the greater use of the left hand to the postural adjustments required for reaching and the instability induced by such postures under the experimental conditions as opposed to foraging when animals are typically quiescent. Left hand use from

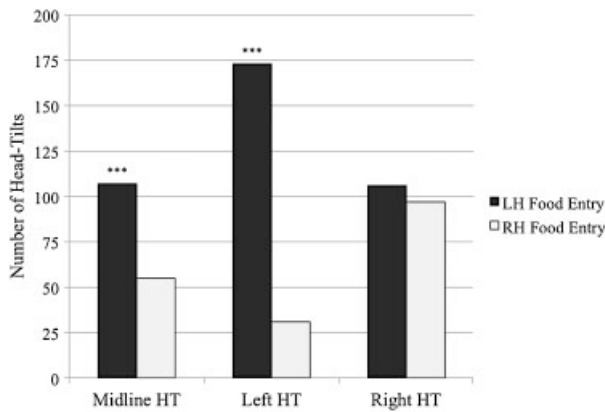


Fig. 3. Number of head-tilts for left and right hand food entry for each head-tilt position. Food entry indicates hand used to place food in the mouth before head-tilt. Asterisks denote significant food entry preferences (χ^2 goodness-of-fit tests, $P < 0.001$). HT = head-tilt, LH = left hand, RH = right hand.

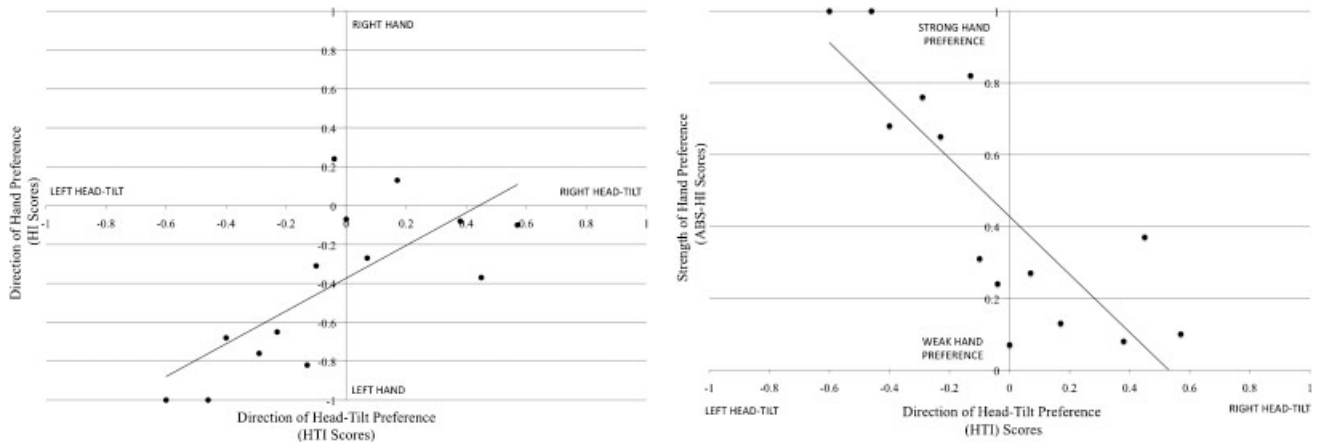


Fig. 4. Direction of head-tilt preference predicted direction of hand preference (left panel) and strength of hand preference (right panel). HTI scores were correlated with HI scores, $r = 0.716$, $P < 0.01$. Left hand use increased as left head-tilts increased. HTI scores were correlated with ABS-HI scores, $r = -0.817$, $P < 0.01$. Hand preference strength increased as left head-tilts increased.

this study averaged 67% ($n = 19$) with lemurs predominantly feeding from a stable sitting position. These findings support the interpretations of Forsythe et al. [1988] that left hand use may be less pronounced in ruffed lemurs when posture is not challenged.

Age is an additional variable thought to affect hand preference in prosimians. Previous studies have suggested a trend of right hand use increasing with age [Forsythe & Ward, 1988; Mason et al., 1995; Ward et al., 1990]. In this study, age was not correlated with direction of hand preference as calculated by HI scores or strength of hand preference as calculated by ABS-HI scores. There was also no effect of age on hand preference direction or strength when young adult and adult lemurs were compared. Notably, infant and juvenile lemurs were not sampled in these data, and we are unable to speculate as to when hand use biases first appear in this species or whether biases are maintained within individuals over the lifespan.

Individual head-tilting preferences were not as robust as the findings for hand use, with only 4 of 14 lemurs significantly lateralized for the head positioning behavior. As a group there was no directional bias for head-tilting. The failure to find a directional bias may be due to the frequency of this behavior in the population over the sampling period. Head-tilting was observed half as frequently as manual feeding, limiting the number of animals with sufficient data for statistical analyses. It may also be the case that strong head biases are only seen in infancy, and weaken or disappear entirely over development. Although these data cannot address infant or longitudinal head-tilting effects, support for this hypothesis comes from human infant data that suggest infant head turning preferences disappear between 3 and 6 months of age [Konishi et al., 1986]. In addition, neonatal lemur head positioning biases, if they exist, could involve simply turning the head preferentially to one side, rather than executing the more extreme head-tilting posture. This in turn could promote an asymmetry in the visual experience of the hands, which has been hypothesized to be the link between head positioning and hand use in human infants [Coryell & Michel, 1978; Michel, 1981]. If the head is more often turned to the left than the right, the infant lemur will view the left hand more than the right and later preferentially use the left hand because of the early biased visual experience. To the best of our knowledge, there are no published studies on lateralized behavior in infant prosimians. Longitudinal studies that follow infant ruffed lemurs from birth would clarify whether head positioning biases are evident in infancy and whether these biases persist, weaken, or disappear in adulthood.

Nonhand use behaviors like head-tilting are important for understanding whether mechanisms

for laterality share the same neural system or operate under different neural systems [Cantalupo & Ward, 2000; Dodson et al., 1992; Larson et al., 1989; Ward, 1991; Ward & Cantalupo, 1997]. The lateral bias of other nonmanual behavior patterns has been examined in prosimians. A left bias was found in bushbabies (*G. senegalensis*) making 180° whole-body turns. However, in contrast to our study, there was no relationship between turning and hand preferences [Larson et al., 1989]. A left bias has also been found in galagos (*G. moholi*) making 180° turns and mouse lemurs (*Microcebus murinus*) making turns less than 180°. No relationship was found between whole-body turning and hand use preferences for either species [Dodson et al., 1992]. In ringtailed lemurs, no group-level preference was found for whole-body turns greater than 135°. At the individual level, however, eight of ten lemurs were concordant for whole-body turn preference and hand preference as measured by reaching [Shaw et al., 2004].

Results from studies of whole-body turning and hand use seem to largely suggest that turning and hand preferences do not share the same neural mechanism. It is possible that these preferences are not explicitly related because whole-body turning is not tied exclusively to feeding. Animals may make whole-body turns in other contexts where the hands are not involved in manipulation. In this study, head-tilting significantly predicted hand preference despite few significant individual head preferences and no population-level preference. From our observations, head-tilting is tied exclusively to feeding and this shared context may explain the predictability found between the two behaviors. The direction of head-tilt preference was positively associated with the direction of hand use preference. In addition, lemurs with stronger hand preferences regardless of direction made more left head-tilts, indicating a relationship between hand lateralization and left head bias. Furthermore, it was not the case that the lemur simply tilted its head in the direction of the hand it had used to put the food item into its mouth. For left head-tilts, there was a strong bias for the left hand to precede the head-tilt. For right head-tilts, however, lemurs were equally likely to use either the right or the left hand before they head-tilted. Head-tilts were also observed after oral food retrievals when no hand had been used to manipulate the food. These data confirm the strong relationship between the left hand and left head-tilting in black and white ruffed lemurs.

The question remains as to why the feeding system would favor a group-level left hand bias, but no bias in head-tilting in black and white ruffed lemurs. MacNeilage et al. [1987] proposed a theory implicating hemispheric specialization in nonhuman primate hand preference. For prosimians specifically, the authors suggest a right hemisphere/left hand

bias in visually guided reaching and a left hemisphere/right hand bias in postural support. Such a division of labor between the hemispheres has adaptive significance for a species like the ruffed lemur, which lives in a niche environment in the high canopy and employs a variety of postures including sitting, standing, suspensory hanging, and clinging during feeding [Britt, 2000]. In contrast, a bias in head-tilting could result in asymmetrical tooth wear or loss and have potential consequences for health and well-being. To date, there are no reports comparing dental wear to behavioral asymmetries in lemurs. However, Cuzzo and Sauther (unpublished data) found no evidence of asymmetric gross dental wear in a small sample of *Varecia* museum specimens ($n = 5$). These museum data seem to support our findings of a lack of head-tilting bias at the population-level. Nevertheless, there was a clear relationship between the left hand and left head-tilting in our data. We suggest that the correspondence between these behaviors promotes efficient whole-body organization [MacNeilage, 2006]. The leftward lateralization seen in feeding may increase brain capacity for other tasks because only one hemisphere is engaged, whereas the other remains available [Vallortigara & Rogers, 2005].

Returning to the data from infant humans and chimpanzees, our results support previous findings showing a link between head and hand use preferences, although the direction of bias differed. In lemurs the direction of the bias was toward the left and in humans and chimpanzees the direction of bias was toward the right. We acknowledge that it is possible that the mechanism linking head and hand preferences in lemurs is different than the mechanism linking similar biases in humans and chimpanzees, but we suggest that a link between behaviors regardless of the direction of bias has advantages for neural organization. By studying patterns of laterality, rather than individual behaviors, we can begin to understand how and why the primate brain is lateralized and how it has changed over evolutionary time.

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