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Hand Use and Gestural Communication in Chimpanzees (*Pan troglodytes*)

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Abstract

Hand use in gestural communication was examined in 115 captive chimpanzees *(Pan troglodytes)*. Hand use was measured in subjects while they gestured to food placed out of their reach. The distribution of hand use was examined in relation to sex, age, rearing history, gesture type, and whether the subjects vocalized while gesturing. Overall, significantly more chimpanzees, especially females and adults, gestured with their right than with their left hand. Foods begs were more lateralized to the right hand than pointing, and a greater prevalence of right-hand gesturing was found in subjects who simultaneously vocalized than those who did not. Taken together, these data suggest that referential, intentional communicative behaviors, in the form of gestures, are lateralized to the left hemisphere in chimpanzees.

Contrary to the historical accounts (Warren, 1980), recent evidence suggests that hemispheric specialization is not unique to humans and can be found for a variety of tasks in numerous species (Bradshaw & Rogers, 1993;Fagot & Vauclair, 1991;Hopkins, 1996b;MacNeilage, Studdert-Kennedy, & Lindblom, 1987;Ward & Hopkins, 1993). One area of investigation in the study of hemispheric specialization has been communication. Specifically, whether animals exhibit similar forms of hemispheric specialization either in their natural communication or in the use of artificial communication systems has been a topic of interest since the earliest reports of laterality in humans (Harris, 1993). With the exception of data on bird song (Nottebohm, 1977), early studies in a variety of animal species failed to report any evidence of hemispheric specialization in communicative functions. In fact, the complete absence of evidence for hemispheric specialization of any form in animals led some to speculate that language and hemispheric specialization evolved de novo in humans (Corballis, 1991;Hamilton, 1977;Warren, 1980).

Notwithstanding, whether communicative behaviors represent a unique class of lateralized behavior similar to that observed in humans remains relatively unstudied but warrants investigation given the inherent interest in linking the evolution of communication with organizational properties of the central nervous system (see Falk, 1987;Hewes, 1973;Kimura, 1993;Passingham, 1982).

In female mice, Ehret (1987) found that the processing of ultrasonic pup sounds were better processed by the left than the fight hemisphere. In Japanese macaques, Peterson, Beecher, Zoloth, Moody, and Stebbins (1978) reported a right-ear advantage in the acquisition of a vocalization discrimination task. Using a more ethological approach, Hauser (1993) recorded

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the movements of the mouth and face when rhesus monkeys were vocalizing and reported that the left half of the mouth and face moved before the fight half. These results were interpreted as evidence of a right-hemisphere asymmetry in the production of facial expressions by rhesus monkeys. In a subsequent study, Hauser and Andersson (1994) reported a fight-sided sound localization bias in the perception of conspecific calls but not heterospecific calls (i.e., bird calls) in free-living rhesus monkeys. These findings were interpreted as evidence of a left-hemisphere asymmetry in the processing of species-specific vocalizations. In terms of artificial communication systems, both language-trained chimpanzees and dolphins have been reported to exhibit a left-hemisphere asymmetry in the processing of meaningful as opposed to nonmeaningful symbols or signs (Hopkins, Morris, & Savage-Rumbaugh, 1991;Morrel-Samuels, Herman, & Bever, 1989).

Previous studies examining lateralization in natural communicative behaviors have emphasized either the perception of auditory stimuli or the production of species-specific vocalizations. As far as we know, there have been no reports of lateral bias in gestural rather than vocal communication in any nonhuman primate species with the exception of preliminary reports on captive bonobos (Hopkins & de Waal, 1995) and chimpanzees (Leavens, Hopkins, & Bard, 1996). Hopkins and de Waal reported that bonobos exhibited more species-typical gestures with their right than with their left hand. In the study by Leavens et al., 3 captive chimpanzees failed to show any strong evidence of laterality in gestures with the exception of those involving a single digit. On the basis of these preliminary results, bonobos appear to gesture with their fight hand whereas chimpanzees do not, suggesting an inherent species difference in communicative abilities between these two species, as has been suggested by some (Savage-Rumbaugh, 1984,1991). However, the gestures observed by Hopkins and de Waal in bonobos were species typical, whereas the gestures studied by Leavens et al. were of a type seldom, if ever, observed in wild chimpanzees (i.e., pointing). The purpose of this study was to examine the occurrence and lateralization in hand use for gestural communication in captive chimpanzees. Of particular interest was the interaction between laterality and the expression of species-typical gestures. If laterality in hand use is contingent on the use of species-typical gestures, then chimpanzees exhibiting food begs should be more likely to use their fight hand than chimpanzees who exhibit gestures that are not species typical (i.e., pointing). Additionally, laterality in gestures in relation to rearing and subject variables was of interest.

Method

Subjects

Subjects were 115 chimpanzees *(Pan troglodytes)* housed at the Yerkes Regional Primate Research Center (YRPRC) in Atlanta, Georgia. There were 50 males and 65 females, ranging in age from 3 to 56 years ($M = 18.8$, $SD = 11.7$). None of the subjects had been language trained. Three of the subjects have been previously reported to point (Anna and Clint by Leavens et al., 1996; Kipper by Tomasello, George, Kruger, Farrar, & Evans, 1985). In terms of rearing histories, 71 subjects were nursery reared, 24 were mother reared, and 20 had unknown rearing histories (see Bard, 1996, for discussion of nursery-rearing practices at YRPRC).

Procedure

The general experimental procedure has been described in detail by Leavens and Hopkins (in press). Two experimenters participated in each trial. Experimenter 1 (El) walked to the outside section of each subject's home cage and placed half of one banana on the ground. The banana was approximately 1 m from the front of the cage and out of reach from the subject. The position of the banana was in line with either the left or the right walls of the subjects' cages, randomized by side across trials. After depositing the banana, E1 departed, whereupon Experimenter 2 (E2) approached the subject and engaged him or her with eye contact and verbal greetings but ignored the banana. If the subjects (a) alternated their gaze between the banana and the experimenter while either vocalizing or gesturing or both, (b) vocalized while emitting a gesture, or (c) gestured, they were immediately given the banana. If none of these behaviors was observed within 30 s of the arrival of E2, the subject was given the banana. To minimize the effect of repeated testing on the specific pattern of lateral bias in gestures, we ensured that each subject received only one 30-s trial. Assignment of the researchers to E1 or E2 was determined by their relative familiarity with each subject, although both researchers were familiar to the chimpanzees because the apes have been subjects in several colony-wide studies of handedness (e.g., Hopkins, 1994,1995).

Behavioral Coding

The specific behaviors of interest that were recorded by E2 are summarized below. First, vocalizations were recorded as either present or absent during each trial. Initially, we attempted to characterize the vocalizations as either food calls or other calls, but the data were eventually collapsed to increase statistical power. The hand initially used to gesture was recorded as left, right, or both. The type of gesture was recorded as either a food beg or pointing. Food begs have been described in wild and captive chimpanzees and involved extended arms directed toward E2 with the fingers and palm of the hand supinated (facing up) and maintained in a “cupped” posture (Berdecio & Nash, 1981;van Hooff, 1973;van Lawick-Goodall, 1968a, 1968b;Plooij, 1978). In our previous research, pointing has been distinguished as whole handed or indexical (see Leavens et al., 1996). In this study, to increase our statistical power, we did not maintain this distinction in pointing and therefore included whole-hand points and indexical points as one class of pointing that was distinct from food begs. It should be emphasized that pointing, as defined in this study, has not been described in wild chimpanzees and appears to develop within the context of captive settings. The exact contextual or training conditions for the acquisition of these types of gestures is at present unknown. Gaze behavior was recorded as (a) gaze alternation (subject looked at both the banana and E2) or (b) no gaze alternation (the subjects looked only at E2, looked only at the fruit, or did not look at either E2 or the banana).

Analyses

Chi-square analyses were used to evaluate hypotheses. To assess the effect of age on laterality in hand use, we divided the sample into two age groups, including (a) juveniles and adolescents (3 to 15 year olds) and (b) adults ($\geq$ 16 years of age). Age classifications were based on data from Goodall (1986). Test-retest reliablity assessments of hand use for gestures were performed on a subset of the chimpanzee sample (20%), with 75% of the sample using the same hand on successive tests.

Results

Overall, 63 of the 115 chimpanzees exhibited a unimanual gesture, with 40 using their fight hand and 23 using their left hand. The proportion of fight- to left-handed chimpanzees differed significantly from chance ($z = 2.15$, $p < .05$). Depicted in Table 1 is the distribution of right- and left-hand use as a function of sex, age, position of the food, type of gesture, rearing history, and whether the subjects vocalized while gesturing. Significant interactions were found between gesture type and hand use, $\chi^2(1, N = 63) = 5.04$, $p < .05$; age and hand use, $\chi^2(1, N = 63) = 4.80$, $p < .03$; and whether or not subjects vocalized and hand use, $\chi^2(1, N = 63) = 4.11$, $p < .05$. Subjects were more likely to exhibit a right-hand gesture for food begs compared with pointing. Older subjects showed greater right-hand use than younger subjects, and subjects who vocalized to E2 were more likely to gesture with their fight hand compared with those who did not vocalize. A borderline significant interaction was found between sex and hand use, $\chi^2(1, N = 63) = 3.21, p < .07$. Seventy-four percent of the females exhibited a right-hand gesture compared with 51% of the males.

Most of the subjects in this study have also served as subjects in previous studies on hand preference measuring either bimanual feeding or coordinated bimanual actions (see Hopkins, 1994,1995). To determine whether the observed lateral biases in gestures were associated with inherent hand preferences, we compared the distribution of hand use in gestures as a function of whether the subjects were classified as left- or right-handed in hand preference on the two aforementioned tasks using Cochran's Q test. No significant interactions were found between lateral bias in gestures and hand preferences for either bimanual feeding or coordinated bimanual actions. Thus, hand use in gestures does not appear to be an artifact of an existing manual specialization for noncommunicative functions.

Discussion

The results of this study indicate that hand use in gestural communication is primarily done by the right hand in captive chimpanzees, particularly for species-typical gestures. Adults were more right-handed than juvenile and adolescent apes, and there was an interaction between hand use and whether or not the apes vocalized while gesturing. Neither the position of the food nor the rearing history of the subjects influenced the distribution of hand use.

There are at least two possible explanations for the observed right-hand use in gestural communication. First, the evidence of right-hand use in gestural communication, particularly for food begs, suggests that an inherent left-hemisphere asymmetry in communicative function may be present in chimpanzees. Moreover, the asymmetry may be specifc to species-typical communicative gestures and not communicative gestures that are an artifact of captivity (i.e., foods begs vs. pointing). It is important to emphasize that most of the gestures between the experimenters and the fruit used by the chimpanzees were accompanied by gaze alternation and, therefore, were intentional and referential in function (see Leavens et al., 1996;Leavens & Hopkins, in press, for discussion). It is not clear whether similar patterns of asymmetry would be present in gestures that were not associated with gaze alternation. Unfortunately, there were too few subjects who gestured but did not exhibit concomitant gaze altemation for us to compare with the gaze-alternating subjects ($n = 7$ [3 left and 4 right]). This comparison will be critical for determining whether the referential nature of the communication is a necessary condition for the execution of right-hand gestures.

An altemative explanation for the right-hand biases in gestures may be related to affect or emotional valence associated with the presence of the food that is otherwise unattainable to the ape. Davidson (1992) proposed that emotions or affective states are differentially processed by each hemisphere, with the right hemisphere controlling negative emotions and the left hemisphere controlling positive emotions. Hopkins and Bennett (1994) previously reported that right-handed chimpanzees approach novel objects significantly faster than non-right-handed chimpanzees, a finding that was interpreted as supporting the Davidson emotional-valence model of hemispheric specialization. In the case of our findings in this study, the presence of the food may have induced a positive emotional valence that resulted in greater preferential use of the right compared with the left hand in the context of interspecies communication. This argument is supported, in part, by the observation that greater right-hand use was associated with the production of vocalizations, which presumably reflected a heightened affective state in the chimpanzees. We made no attempt to measure the affective state of the animals (i.e., assessing the rate or intensity of the vocalizations) and therefore cannot directly address this issue. Notwithstanding, most of the vocalizations were either food barks or attention-getting sounds, calls that have positive affective valence. It is clear that further research is needed to analyze whether the observed findings are due to the affective nature or the referential function of the communicative signal.

We do not believe that our results are the basis of a simple reaching bias in the chimpanzees for two reasons. First, we failed to find an association between hand use for gestures and previously published findings on preference for either bimanual feeding or coordinated bimanual actions (see Results section). If hand use for gestural communication were an artifact of an inherent manual specialization, then a significant positive association should have been found. Second, several studies in monkeys and apes have reported that hand use in reaching is influenced by the position of the food (see Lehman, 1993;Welles, 1976) such that primates will typically reach with the ipsilateral hand. We did not find an interaction between hand use and the position of the food, which would be predicted if the effects were simply frustrated reaches on the part of the apes.

A borderline significant interaction was found between sex and hand use, with female chimpanzees using their right hand more often to gesture compared with male chimpanzees. Previous evidence of sex differences in lateral bias in chimpanzees has indicated greater right-sided biases for infant females in hand-to-mouth behavior (Hopkins & Bard, 1993), head orientation during sleeping (Hopkins & Bard, 1995), and leading limb in locomotion (Hopkins, Bard, & Griner, 1997). Whether the same neurological mechanisms account for the expression of sex differences in these different measures of laterality remains unclear.

The interaction between hand use and whether or not the chimpanzees vocalized warrants some discussion. Studies in human participants have found greater right-hand activity when people are talking than when they are not (Dalby, Gibson, Grossi, & Schneider, 1980;Hampson & Kimura, 1984). These findings have been taken as support for the “overflow” hypothesis of hemispheric activation, which proposes a spread of neural activity from motor speech areas to motor limb areas in the left frontal cortex during speech acts (Kinsbourne & Hicks, 1978). Given that more chimpanzees gestured with their right hand while vocalizing, one interpretation would be that a similar overflow mechanism is evident in chimpanzees. Alternatively, the overall greater right-hand use might be associated with levels of arousal in the chimpanzees. Hopkins and Bard (1993) previously reported an association between lateral bias in hand-to-mouth behavior and arousal. Greater right-sided biases in hand-to-mouth were associated with lower arousal. The right-sided gesturing by the chimpanzees may be associated with reduced arousal in the context of the presentation of food that is out of their reach. These two alternative explanations for the observed association between hand use and vocal behavior warrant further study.

Finally, an interaction was found between age and hand use. Older chimpanzees were more likely to gesture with their right hand compared with younger chimpanzees. These data suggest maturational processes in the manifestation of laterality, a finding consistent with other studies of hand use in the YRPRC chimpanzees (Hopkins, 1994,1995), as well as other studies of laterality in communicative behavior (Hauser & Andersson, 1994). Notwithstanding, our developmental findings are limited by the fact that the youngest animals were less likely to exhibit any gestures (see Leavens & Hopkins, in press). Moreover, all of the chimpanzees of unknown rearing history were likely wild caught, and therefore age is to some degree confounded with rearing history. Thus, the developmental findings should be interpreted with caution.

In summary, gestural communication is lateralized in captive chimpanzees. The data represent the first systematic effort to examine laterality and communication in apes, and by no means have all dimensions of this relation been exhausted. Whether this behavioral asymmetry has neurobio-logical correlates remains unknown. Chimpanzees have been reported to exhibit neuroanatomical asymmetries in areas of the brain that are associated with language in humans (Hopkins, 1996a;Yeni-Komshian & Benson, 1976), and it is possible that these areas are associated with gestural communication in apes. However, in the absence of direct studies mapping communicative behavior in relation to different brain areas, this hypothesis remains largely speculative. With the development of imaging techniques such as magnetic resonance imaging and positron emission tomography, these hypotheses may be testable soon.

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Table 1

Distribution of Hand Use in Gestural Communication

	Hand use			
Variable	**Left**	**Right**	***z* score**	**$\chi^2(1, N = 63)$**
Sex				3.21
Male	14	15	0.19	
Female	9	25	2.75*	
Gesture type				5.04
Food beg	3	16	2.98*	
Pointing	20	24	0.60	
Food position				0.55
Left	12	17	0.09	
Right	11	23	1.91	
Vocalization				4.11
Yes	5	19	2.86*	
No	18	21	0.48	
Age				4.80
3–15 years	14	13	−0.19	
> 15 years	9	27	3.00*	
Rearing				0.25
Mother	10	20	1.82	
Nursery	13	20	1.22	

[*] $p < .01$.