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Grip Morphology and Hand Use in Chimpanzees (*Pan troglodytes*):

Evidence of a Left Hemisphere Specialization in Motor Skill

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Abstract

Three experiments on grip morphology and hand use were conducted in a sample of chimpanzees. In Experiment 1, grip morphology when grasping food items was recorded, and it was found that subjects who adopted a precision grip were more right-handed than chimpanzees using other grips. In Experiment 2, the effect of food type on grasping was assessed. Smaller food items elicited significantly more precision grips for the right hand. In Experiment 3, error rates in grasping foods were compared between the left and right hands. Significantly more errors were made for the left compared with the right hand. The cumulative results indicate that chimpanzees show a left-hemisphere asymmetry in motor skill that is associated with the use of precision grips.

Hemispheric specialization refers to the extent to which either the left or right hemisphere is dominant for specific motor, cognitive, perceptual, or emotional processing (Springer & Deutsch, 1998). Although clearly an oversimplification, in humans, the left hemisphere has been reported to be dominant for speech and language processing as well as for motor skills, whereas the right hemisphere is specialized for processing visual-spatial problems as well as affective valence and emotions (Hellige, 1993). Hemispheric specialization in humans has been linked to the evolution of a variety of complex skills including tool use, handedness, gestural communication, and language (Boesch & Boesch, 1993; Bradshaw & Rogers, 1993; Hewes, 1973; Marzke, 1997). Therefore, whether nonhuman animals exhibit hemispheric specialization for any abilities has been a topic of considerable historical and contemporary interest in psychology, neuroscience, and a host of other scientific disciplines (Harris, 1993).

Recent studies in a host of vertebrates suggest that there is evidence of left and right hemispheric specialization for some perceptual, emotional, and cognitive functions (Bisazza, Rogers, &

Vallortigara, 1998; Hopkins & Fernandez-Carriba, 2002; Rogers & Andrews, 2002; Vallortigara, Rogers, & Bisazza, 1999). For example, in nonhuman primates, studies suggest a left hemisphere specialization in the processing of auditory stimuli including pure tones and species-specific vocalizations (Dewson, 1977; Hauser & Andersson, 1994; Heffner & Heffner, 1984; Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978; Pohl, 1983, 1984). In nonhuman primates, there is also good evidence of right hemisphere specialization in individual recognition and discrimination of species-specific facial expressions (Hamilton & Vermeire, 1988; Vermeire & Hamilton, 1998). On the whole, these data indicate that language is not a necessary condition for the expression of hemispheric specialization in animals, at least as it pertains to perceptual, cognitive, or emotional processing. However, for motor functions such as hand skill or hand preference, there remains considerable debate over whether animals and, in particular, nonhuman primates exhibit hemispheric specialization (Ettlinger, 1988; Hook-Costigan & Rogers, 1997; Hopkins, 1999a; McGrew & Marchant, 1997; Warren, 1980).

In humans, clinical and experimental studies indicate that the left hemisphere is specialized for the control of motor skill. There are three bodies of data that support this view. First, approximately 85–90% of humans report themselves as being right-handed (Annett, 1985; Porac & Coren, 1981), and behavioral studies indicate that the right hand typically performs better than the left on tasks assessing motor skill (Annett, 1992, 1998; Peters, 1991). Second, individuals with lesions to the left hemisphere show greater impairment (e.g., apraxia) on tasks assessing motor skill and planning (Harrington & Haaland, 1994; Kimura, 1993; Kimura & Archibald, 1974). Third, recent neurophysiological studies have reported that motor thresholds elicited by transcranial magnetic stimulation (TMS) in the primary motor cortex of the hemisphere contralateral to the preferred hand are lower than in the ipsilateral hemisphere (Macdonell et al., 1991; Triggs, Calvanio, & Levine, 1997). Moreover, the application of TMS to the premotor cortex of humans has been shown to disrupt planned motor actions, particularly in the left hemisphere (Schluter, Rushworth, Passingham, & Mills, 1998). Taken together, these data suggest that the left hemisphere is dominant for the planning and execution of motor processes involved in skilled movements.

From a comparative perspective, the most common approach in evaluating whether nonhuman primates exhibit hemispheric specialization in motor functions has been to test for *population-level handedness*. Population-level handedness refers to instances in which a significant statistical majority of the subjects within a sample exhibit preference of the same hand for a specific task. There have been a number of studies on hand preference for a host of behavioral measures in various nonhuman primate species (see Fagot & Vauclair, 1991; Hopkins, 1996; MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Marchant & McGrew, 1991; Ward & Hopkins, 1993). Some recent studies have clearly demonstrated evidence of population-level hand preference in some species for certain measures, but the results have not always been consistent between laboratories or between species on which comparable or identical measures have been used. For example, for measures of coordinated bimanual actions, gorillas (Byrne & Byrne, 1991) and chimpanzees (Colell, Segarra, & Sabater-Pi, 1995; Hopkins, 1995) have been reported to show population-level right-handedness. In rhesus and capuchin monkeys, some studies report population-level right-handedness for coordinated bimanual actions (Spinozzi, Castornina, & Truppa, 1998; Westergaard & Suomi, 1996), whereas others do not (Westergaard, Champoux, & Suomi, 1997). However, one problem with inferring hemispheric specialization for motor skill from hand preference data is that the two functions may be somewhat independent (e.g., Andrews & Rosenblum, 1994; Hopkins, Washburn, Berke, & Williams, 1992). In other words, in nonhuman primates, it has not been demonstrated that preference for use of a specific hand represents an inherent bias in skill for that hand on the task in question. This is particularly relevant in light of the fact that postural and task demands seem to exert significant effects on the expression of hand preference. What is needed to infer hemispheric specialization at the behavioral level is the comparison of the two hands on

measures of motor skill rather than hand preferences per se. Unfortunately, very few studies have examined differences in motor skill between the left and right hands, and most have been largely descriptive involving a limited number of subjects and species (Andrews & Rosenblum, 1994, 2001; Butler, Stafford, & Ward, 1995; Ettlinger, 1988; Frigaszy & Adams-Curtis, 1993; Hopkins, Washburn, & Rumbaugh, 1989; Lacreuse & Frigaszy, 1997; McGrew, Marchant, Wrangham, & Klein, 1999; Preilowski, 1993; Rigamonti, Previde, Poli, Marchant, & McGrew, 1998).

The purpose of this study was to evaluate the relation between hand preference, hand skill, and grip morphology in chimpanzees. From a primate perspective, the remarkable manipulatory skills of humans have been attributed to the evolution of individual digit control and an opposable thumb (Frigaszy, 1998). In terms of grip morphology, much research has focused on the abilities of different primates to grasp objects, the types of grips employed in grasping objects, and how grasping relates to hand morphology and neural innervation of the digits (Christel, 1993; Christel, Kitzel, & Niemitz, 1998; Costello & Frigaszy, 1988; Jones-Engel & Bard, 1996; Napier, 1960; Welles, 1976). The most common distinction in grip morphology is between *power* and *precision grips* (Marzke, 1997). Power grips occur when “the object is held as a clamp between the flexed fingers and the palm, counter pressure being applied by the abducted thumb” (Napier, 1960, p. 648) and are primarily used in the application of force. Power grips are used by nearly all primate species (e.g., Welles, 1976). In contrast, precision grips occur when “the object is gripped between the palmar aspect of the terminal phalanx of the finger or fingers and the thumb” (Napier, 1960, p.648). With respect to the precision grip, the emphasis on the use of the thumb and index finger in grasping was no doubt stimulated by the early claims that only humans made true precision grips, which were defined as tip-to-tip opposition of the thumb and index finger (Napier, 1960). However, recent studies clearly challenge this view as a number of species have been reported to demonstrate true precision grips (for reviews, see Butterworth & Itakura, 1998; Christel, 1993, 1994; Christel & Frigaszy, 2000; Jones-Engel & Bard, 1996), although the frequency of occurrence is relatively low compared with other gripping preferences. This may be due to morphological differences between the hands of humans and other primates (Tuttle, 1969, 1981).

With respect to hand preference and grip morphology, recent studies suggest that phylogenetic and individual differences in grip morphology may be associated with hand preference. For example, Christel (1993) reported that apes were more right-handed than Old and New World monkeys for simple reaching and that this was possibly due to the greater use of precision grips by great apes. Within New World monkeys, Costello and Frigaszy (1988) found that capuchin monkeys were more right-handed and used more precision grips when reaching for food than squirrel monkeys. Tonooka and Matsuzawa (1995) found that right-hand use in reaching was higher for precision compared with nonprecision grips in a sample of 80 captive chimpanzees. In their study, precision grips were defined as those in which the thumb and index finger were used to grasp a small piece of food.

In the current study, three experiments on grip morphology and hand use are reported in a sample of captive chimpanzees. The principal aim of the initial study was to evaluate the distribution of spontaneous grip preferences in relation to hand use. In many ways, Experiment 1 was an attempt to replicate the findings of Tonooka and Matsuzawa (1995) in a larger sample of chimpanzees but using a simpler coding scheme for grip morphology. In Experiment 2, the influence of food size and texture on grip morphology and hand use was tested. Specifically, we hypothesized that for food items that were smaller and more difficult to grasp, significantly greater use of thumb-index responses would be observed. Moreover, if the left hemisphere is specialized for motor skill, then this effect would be more pronounced for the right compared with the left hand. Finally, in Experiment 3, error rates in gripping small food items were compared between the left and right hands to evaluate whether the two hands differed in

performance. All prior studies on grip morphology and hand use have focused on preference rather than performance of each hand when grasping objects. If the left hemisphere is dominant for motor skill, then it can be hypothesized that fewer errors in gripping will be made for the right compared with the left hand. Furthermore, accuracy for grasping small objects should be significantly better when subjects use a precision compared with a nonprecision grip. Finally, performance differences in gripping between the hands should be associated with hand preference.

Experiment 1

Method

Subjects—Subjects were 140 captive chimpanzees (*Pan troglodytes*) housed at the Yerkes Regional Primate Research Center (YRPRC) of Emory University. There were 79 females and 61 males, ranging in age from 3 to 39 years ($M = 14.81$, $SD = 9.77$). Of the 79 females, there were 49 *mother-reared* and 30 *nursery-reared* subjects. Of the 61 males, there were 22 mother-reared and 39 nursery-reared subjects. Mother-reared chimpanzees were those reared by their biological, conspecific mother for more than 30 days of life. Nursery-reared subjects were those which were brought to the YRPRC nursery before 31 days of life. The standard protocol for hand-rearing chimpanzees has been described in detail elsewhere (Bard, 1996).

Procedure—Hand use and grip morphology was recorded for simple reaching. On each trial, a raisin was thrown into the subject's home cage. The raisin was thrown by the experimenter to a location at least 3 m from the focal subject so that the chimpanzees had to locomote to position to the raisin, pick up the raisin, and bring it to their mouth for consumption. When the chimpanzee acquired the raisin, the experimenter recorded both the hand used (left or right) and the grip type used to grasp the raisin. Grip type was classified in three ways that were similar to those employed by previous investigators (Butterworth & Itakura, 1998; Christel, 1993; Tonooka & Matsuzawa, 1995) and included *thumb-index*, *middle-index*, and *single digit*. Any gripping response in which the subjects adducted the thumb to the index finger to grip the raisin was recorded as a thumb-index response. Reaching was recorded as a middle-index grip when the subjects grasped the raisin between the index and middle finger with the hand either in a prone or supine position. Thumb-index and middle-index grip types were by far the most common, but, occasionally, subjects engaged in what was recorded as single-digit responses. Single-digit responses were instances in which the chimpanzees used one finger to press down hard enough on the raisin so that it stuck while being taken to the mouth.

Each chimpanzee was tested in the outdoor portion of its home cage. For subjects housed at the YRPRC Main Center, the outdoor cages measured 6 m $\times$ 3 m $\times$ 3 m. For the chimpanzees housed at the YRPRC Field Station, the outdoor compound measured 50 m $\times$ 50 m in dimension. One, and only one, reaching response was recorded each trial to assure independence of data points (see McGrew & Marchant, 1997, and Hopkins, 1999b, for contrasting views). Thus, raisins were not randomly scattered in home cages, but rather an individual raisin was thrown into cages and subjects retrieved the raisin before another was thrown into the cage. Subjects were required to locomote at least three strides between reaching responses to maintain postural readjustment between trials. Approximately 15–30 s separated each trial, which provided adequate time for the subjects to locomote to the food and consume it. A minimum of 50 responses was collected from each subject, and there was a range of 50–84 responses for the sample ($M = 53.75$, $SD = 7.87$).

Data analysis—For each subject, the total number of left- and right-hand responses made for each grip type was summarized. Handedness was characterized in three ways. First, an overall handedness index (SUM-HI) was calculated on the basis of the total number of left (L)- and right (R)-hand responses. The number of left-hand responses was subtracted from the

number of right-hand responses, and that result was divided by the total number of responses: $[(R - L)/(R + L)]$. Secondly, for each subject, a handedness index was calculated for left- and right-hand responses for the thumb–index and middle–index grips. Both the thumb–index and middle–index asymmetry coefficients were derived following the same formula that was used to derive the SUM-HI score. Lastly, binomial z scores were derived on the basis of the frequencies in hand use, and these values were used to classify subjects as left-handed, ambiguously handed, or right-handed. Subjects with z scores that were either below -1.95 or above 1.95 were classified as left- or right-handed, respectively. Subjects with z scores between -1.96 and 1.96 were classified as ambiguously handed.

Results

Grip preferences—In Table 1, we have depicted the relative frequencies of each grip type for male and female subjects. A mixed-model analysis of variance (ANOVA) revealed a significant main effect for grip type, $F(2, 276) = 78.3, p < .001$, and a significant two-way interaction between sex and grip type, $F(2, 238) = 9.32, p < .001$. Subsequent post hoc analyses using independent-samples t tests with Bonferroni's correction procedure indicated that males used the thumb–index grip proportionally more often than females, $t(138) = 2.89, p < .001$, whereas females used the middle–index grip proportionally more often than the males, $t(138) = -3.27, p < .001$. No sex differences were found in the proportion of single-digit grips. In light of the fact that over 97% of the responses were either thumb–index or middle–index grips, subsequent analyses on hand use in relation to grip type were restricted to these two grip types.

Hand preference—On the basis of the individual z scores, there were 26 left-, 51 ambiguously, and 63 right-handed chimpanzees—a distribution that differs significantly from chance, $\chi^2(2, N = 140) = 15.27, p < .01$. The number of left-handed subjects was significantly less than the number of right-handed subjects, $\chi^2(1, N = 89) = 15.38, p < .01$, and ambiguously handed subjects, $\chi^2(1, N = 77) = 8.12, p < .01$. No significant difference was found in the number of ambiguously and right-handed subjects. Two, 2×2 chi-square tests of independence were performed to evaluate whether rearing history and sex influenced the distribution of hand preference. No significant interactions were found. In addition to the categorical data, population-level asymmetries were assessed using a one-sample t test based on the SUM-HI scores. The overall mean handedness index was .11, and this value differed significantly from zero, $t(139) = 3.25, p < .01$. The influence of sex and rearing history on the overall handedness index was evaluated using a between-group-design ANOVA. No significant main effects or interactions were found.

Grip type and hand preference—For this analysis, a mixed-model ANOVA was performed. Hand preference classification was the between-group variable (left, ambiguous, right), and the handedness index scores for the thumb–index and middle–index grip was the repeated measure. A significant interaction was found between hand preference classification and handedness scores for thumb–index and middle–index grips, $F(2, 115) = 3.69, p < .05$. The mean SUM-HI scores for thumb–index and middle–index grips in left-, ambiguously, and right-handed subjects can be seen in Figure 1. No significant differences in SUM-HI scores for each grip type were found in left- and right-handed subjects. However, in ambiguously handed subjects, SUM-HI scores for thumb–index responses were significantly higher (or more right-handed) than SUM-HI scores for middle–index grips, $t(42) = 3.09, p < .01$.

One limitation of this analysis is that the number of observations varied widely between subjects as a function of grip type. This was due in large part to the fact that nearly all of the subjects showed a dominant grip preference. Thus, a second analysis was conducted to test whether the SUM-HI scores for thumb–index and middle–index grips were significantly different. Separate SUM-HI scores were calculated for the thumb–index and middle–index

grip, irrespective of the hand preference of the subjects. Only subjects with six or more responses for each grip type were included in this analysis ($n = 70$). A paired-sample t test revealed a significant difference in the handedness index score $t(69) = 2.33, p < .01$. The mean SUM-HI scores for thumb–index and middle–index grips were .245 (SE = .05) and .035 (SE = .07), respectively.

Correlation between age, grip morphology, and hand preference—Pearson product–moment correlations were performed between age and the proportion of thumb–index responses, SUM-HI scores, and the absolute value of the SUM-HI score. A significant correlation was found between age and the proportion of thumb–index responses ($r = -.194, df = 138, p < .05$). Older subjects exhibited proportionally fewer thumb–index responses than younger subjects. A significant negative correlation was also found between age and the SUM-HI scores ($r = -.232, df = 138, p < .05$). Older subjects had more leftward SUM-HI scores than younger subjects. No significant association was found between age and strength of hand preference.

Discussion

The results from Experiment 1 indicate that hand preferences are associated with grip morphology. Chimpanzees that adopt a thumb–index grip style are more right-handed than subjects that do not. Moreover, for subjects that do not show a dominant grip morphology, thumb–index responses were significantly higher than for middle–index responses. Finally, older subjects were less likely to use a thumb–index grip compared with younger subjects.

The results from this study were, to some extent, consistent with the findings by Tonooka and Matsuzawa (1995). Tonooka and Matsuzawa reported a difference in the distribution of grip type as a function of hand use in a sample of 80 captive chimpanzees. Individual data were reported in their article, allowing for a direct comparison between our results and those reported by Tonooka and Matsuzawa. The data from Table 1 in the Tonooka and Matsuzawa article were entered into a spreadsheet. Tonooka and Matsuzawa made a greater distinction in grip types in their study than we did in our study, and we therefore collapsed data from their study such that only gripping responses that were identical to ours were considered. Specifically, Tonooka and Matsuzawa made a distinction between radial–palmar grasps, imprecise grips, and pincer grips, all of which involved various aspects of the use of the thumb and index finger. Thus, these three grip types were collapsed and considered to be the same as our thumb–index response. Tonooka and Matsuzawa considered the middle–index grip as a separate category, and their definition was identical to ours.

Using the Tonooka and Matsuzawa (1995) data, we derived handedness indexes for responses using either the thumb–index or the middle–index grip. In the initial analyses, the handedness index scores for thumb–index and middle–index responses were compared using a paired-sample t test. A significant difference in SUM-HI values was found between grip type, $t(55) = 2.36, p < .05$. The mean SUM-HI values for each grip type can be seen in Figure 2. For comparison, the comparable data from this study are also shown in Figure 2. The YRPRC apes were more right-handed than the chimpanzees in the Tonooka and Matsuzawa study, but the relative differences in SUM-HI scores for thumb–index and middle–index grip types were nearly identical in the two data sets (M difference = 0.16, respectively). It is not clear why the YRPRC chimpanzees had an overall higher SUM-HI score than the chimpanzees in the Tonooka and Matsuzawa study, but some methodological differences did exist. Notably, individual responses to a single raisin thrown in the cage were recorded in this study, whereas many raisins were spread out on a floor in the Tonooka and Matsuzawa study.

The findings from Experiment 1 also differ from two previous reports on hand use and simple reaching in the YRPRC sample of chimpanzees. Neither Hopkins (1993) nor Wesley et al. (in

press) reported population-level right-handedness for simple reaching in samples of the YRPRC chimpanzees. One potential explanation for the different findings may be in the type of food used. In the previous studies, larger, whole unshelled peanuts were used as the food, whereas smaller sized raisins were used in this study. Perhaps the smaller raisins elicited more precision grips (i.e., thumb index) and therefore more right-hand use than the larger, whole peanuts used in the previous studies. We tested this hypothesis in Experiment 2.

The fact that within-subject variation in hand use can be accounted for by grip morphology in both this study and the report by Tonooka and Matsuzawa (1995) clearly suggests that the left hemisphere is specialized for motor skill. This explanation assumes, however, that adopting the thumb–index grip confers some advantages over the middle–index grip in terms of performance. Unfortunately, this issue was not addressed in Experiment 1. Thus, a second experiment was conducted in which food texture was manipulated to selectively increase the probability of the use of thumb–index grips. Specifically, hand use and grip morphology were examined for two foods varying in texture and adhesive qualities. The hypothesis was that if smoother, less adhesive foods are more difficult to grasp compared with less smooth and more adhesive foods, then thumb–index responses should be significantly more frequent than for the smoother, less adhesive food. Moreover, if the left hemisphere is dominant for fine motor control, then increased thumb–index responses should be more pronounced for the right compared with the left hand.

Experiment 2

Method

Subjects—In Experiment 2, there were 112 chimpanzees, including 49 males and 63 females. All of the subjects were housed at the YRPRC Main Center or Field Station of Emory University and had participated in Experiment 1. The sample size in this experiment was slightly smaller than in Experiment 1 because some subjects were not available for testing owing to their use on other protocols. In addition, some of the chimpanzees would not eat the peanuts and therefore were excluded from this experiment. Subjects ranged from 3 to 39 years of age ($M = 19.54$, $SD = 9.74$).

Procedure—The procedure was similar to Experiment 1. Hand use and grip morphology were recorded for 25 responses for each of two foods including raisins and shelled peanuts. The raisins were very sticky and approximately $13\text{ mm} \times 10\text{ mm} \times 6\text{ mm}$ in size. Shelled, halved raw peanuts were used as the second food item. The peanuts were removed from their shell, and the individual kernel was then divided along the natural fissure of the peanut. When split in half, the peanut kernel measured approximately $15\text{ mm} \times 9\text{ mm} \times 5\text{ mm}$ in dimension. In addition to the small differences in size, the shelled peanut kernels also differed in their texture from the raisins in that they were very smooth with no adhesive qualities like the raisins. The lack of adhesive quality of the peanut kernels made them much more difficult to grasp than the raisins.

Each subject received 25 trials with each food type. Presentation of the different food types was counterbalanced across subjects. All 25 trials were presented for one food type before testing with the second food began. As with Experiment 1, on each trial, a single peanut or raisin was thrown into the cage, and the subject was required to walk to the location of the food and pick it up. The hand used (left, right) and the grip employed (thumb index, middle index, single digit) was recorded on each trial following the same protocol and operational definitions as those employed in Experiment 1.

Results

Grip type and food—In the initial analysis, the frequency of each grip type was examined as a function of food type. A mixed-model ANOVA was performed with food type (raisin, peanut) and grip type (thumb–index, middle–index, single digit) as the repeated measures, while sex (male, female) served as the between-group variable. We found a significant two-way interaction between grip type and food, $F(2, 220) = 22.01, p < .001$. Subsequent pair-samples t tests revealed that the number of thumb–index responses, $t(111) = 3.86, p < .001$, and single-digit responses, $t(111) = 3.76, p < .001$, were significantly higher for peanuts contrasted with raisins. In contrast, the number of index–middle responses was significantly higher for the raisins contrasted with peanuts, $t(111) = -5.97, p < .001$. The post hoc t tests were significant even after adjusting for the number of analyses performed using Bonferroni's correction procedure. The mean number of responses for each grip type and food are shown in Table 2. No other main effects or interactions were found.

Hand use—In the next analysis, we compared hand use for peanut and raisin responses within each grip type. This analysis was restricted to the thumb–index and middle–index responses because they accounted for over 97% of the responses. For the thumb–index and middle–index responses, a $2 \times 2 \times 2$ mixed-model ANOVA was performed with food (peanut, raisin) and hand (left, right) serving as repeated measures, while sex served as the between-group variable. For the thumb–index responses, a significant two-way interaction was found between hand use and food type, $F(1, 110) = 3.89, p < .05$. Post hoc analyses indicated that the number of right-hand responses for peanuts was significantly higher than all other conditions (see Figure 3). For the middle–index responses, no other significant main effects or interactions were found.

Correlates with age—As with Experiment 1, age was correlated with both the frequency and handedness index of the thumb–index responses using a Pearson product–moment coefficient. In terms of the proportion of thumb–index responses, no significant correlations were found between age and the proportion of thumb–index responses for peanuts ($r = -.101, df = 110, ns$) and raisins ($r = -.171, df = 111, ns$). No significant correlations were found between age and the handedness indexes based on thumb–index responses for either the peanuts or raisins. Similarly, no significant correlations were found between age and strength of thumb–index asymmetries for both peanuts and raisins.

Discussion

Results from Experiment 2 indicated that grasping the more slick peanut halves elicited significantly more thumb–index responses than grasping a raisin, particularly for the right hand. This supports the interpretation that food textural affordance has a significant influence on grip morphology and hand preference in chimpanzees, a result consistent with previous reports (Jones-Engel & Bard, 1996; Welles, 1976). In short, food items that are more difficult to grasp elicit the use of more thumb–index responses than food items that are less difficult to grasp. The results further support the interpretation that the left hemisphere is dominant for motor skill in chimpanzees because increases in thumb–index responses were higher for the right compared with the left hand. One limitation of Experiment 2 was the lack of performance measures in grasping, despite our own observations of considerably greater difficulty in grasping the peanut compared with the raisin. Specifically, it was observed during Experiment 2 that many of the chimpanzees had to make several gripping attempts before they successfully picked up and ate the peanut compared with the raisin. Oftentimes, this required that the chimpanzees shift from a middle–index or single-digit response to the use of a thumb–index grip in order to grasp the peanut. Moreover, shifting between middle–index and single-digit responses to a thumb–index response seemed to occur more often with the left compared with the right hand than vice versa. In other words, it appeared that if a chimpanzee was having difficulty grasping the peanut using a single-digit or middle–index response, it would switch

to the use of a thumb–index grip in order to successfully pick up the peanut. In contrast, it was less often observed that chimpanzees having difficulty grasping a peanut with a thumb–index response would switch to the use of a single-digit or middle–index grip type. No attempt was made in Experiment 2 to quantify these observations, so a third experiment was performed.

In Experiment 3, error rates of the left and right hand when grasping small food items were compared. In addition, within-trial variation or shifting in grip type was quantified across subjects. Two hypotheses were tested. First, if the thumb–index response is a more effective grip technique, then (a) fewer errors should be made for this grip type and (b) shifting from a middle–index and single-digit response to a thumb–index response should be more prevalent than the opposite condition. Second, if the left hemisphere is dominant for motor skill in grasping, then fewer errors should be made for the right compared with the left hand.

Experiment 3

Method

Subjects—There were 132 (58 male and 74 female) chimpanzees in this experiment. Subjects housed at both the Yerkes Regional Primate Research Main Center and Field Station were used in this experiment. As with Experiment 2, the chimpanzees' willingness to eat the peanuts was also a factor in determining which subjects were used in this experiment. Subjects ranged in age from 3 to 39 years ($M = 18.10$, $SD = 9.10$).

Procedure—As in Experiment 2, plain, raw peanuts were removed from their shells and split in half. The peanuts were then thrown into the subject's home cage. Because the emphasis of this particular experiment was on obtaining responses with each hand from each subject, the subjects were not required to locomote to the peanut in order for the response to be recorded. Instead, the peanut halves were dropped next to one of the subject's hands, thus encouraging the subject to use one hand over the other. During each test session, testing continued until exactly 10 responses with each hand had been obtained from the subjects. The experimenter watched as the subject attempted to pick up the peanut and noted the sequence of grip types attempted in grasping the food item. Grip types were categorized in the same way as in Experiment 1 and Experiment 2. An error was recorded when the subjects attempted to grasp but dropped the peanut or failed to grasp the peanut from the floor during their attempt. If at any point the subject switched hands or used its mouth to obtain the peanut, the trial was not included. These behaviors were observed very infrequently (constituting less than 3% of the responses); therefore, they were not recorded for consideration in subsequent analyses. However, if the subjects switched grip types within a trial using the same hand, then these data were noted on the scoring sheet. This behavior did occur with some frequency and therefore was of interest in the context of manual performance in grasping. In other words, within a trial, the subjects could shift from a single-digit to thumb–index response or vice versa, and this type of response was characterized on the data sheet. Data were collected in two test sessions with the first 20 responses (10 from each hand) being recorded over a 1-week period. The second test session took place 3 weeks later during which time the second set of data were collected. Testing each subject took approximately 10 min to complete, depending on how difficult it was to get the subjects to use their hands to grasp the food items. Some subjects were much more perseverative in their hand use and therefore required more presentations of the food items before obtaining the needed responses from each hand. Trials were separated by at least 15 s, which gave the subjects time to consume the peanut between trials. During testing, the peanuts were thrown to either side of the subject's body in a random order.

Data analysis—Grasping accuracy was characterized two ways. The first approach was to calculate the number of trials out of a possible 20 trials on which the subjects made an error. The second accuracy measure was derived by summing the total number of errors for each

hand. The second measure differed from the first in that subjects could make more than one error on a given trial and we sought to consider all errors as a separate measure of skill from a general accuracy score.

Results

Error analysis and hand use—In the initial analysis, two ANOVAs were performed. Hand was the within-subject variable (left, right), while sex (male, female) was the between-group variable. For the first analysis, the number of trials on which an error was made served as the dependent variable. For the second analysis, the total number of errors served as the dependent variable. For the number of trials, significant main effects for hand, $F(1, 125) = 14.20, p < .001$, and sex, $F(1, 125) = 7.77, p < .001$, were found. For the second analysis, the results were nearly identical with significant main effects for hand, $F(1, 125) = 15.98, p < .001$, and sex, $F(1, 125) = 6.78, p < .001$. In Figure 4, we have depicted the mean error rates for the left and right hand for each dependent measure. In Table 3, we have listed the mean error rates for males and females for each dependent measure. For both measures, there were significantly more errors with the left compared with the right hand. Males made significantly more errors than females for both measures.

Error analysis and grip morphology—In the initial analysis, error rates were compared between hands, irrespective of the type of grip used by the subjects. In this analysis, the values for each grip type were averaged for each hand and compared using a repeated-measure ANOVA. Specifically, the number of errors made for each grip type was divided by the total number of attempted responses. The error rates were calculated separately for each hand and then averaged for each grip type. For this analysis, grip type was the repeated measure and sex was the between group variable. A significant main effect for grip type was found, $F(2, 74) = 17.69, p < .001$. The mean error rates for each grip type are shown in Figure 5. Error rates were lowest for thumb–index responses followed by middle–index and single-digit responses. One limitation of the ANOVA was that the analyses were limited to subjects that exhibited responses for all three grip types ($n = 74$). This reduced statistical power and did not fully capture the extent of variation in grip type and performance. Thus, a second set of analyses were performed using correlated t tests. From this analysis, the error rates for thumb–index responses were significantly lower than middle–index responses, $t(80) = 2.24, p < .01$, and single-digit responses, $t(52) = 7.23, p < .001$. Middle–index responses were also significantly lower than single digit responses, $t(37) = 3.39, p < .001$. All of these effects were significant even after adjusting alpha using Bonferroni's correction procedure to guard against Type I error.

Within-trial variation in grip morphology—In addition to the overall analysis of error patterns, variation in grip morphology within a trial was analyzed as a means of further examining motor skill. For each subject and trial, we recorded whether the chimpanzee shifted from either a single-digit or middle–index grip to a thumb–index grip. In addition, we recorded the number of occurrences in which subjects shifted from a thumb–index response to either a middle–index or single-digit response. These data can be seen in Table 4. Binomial z scores indicated that shifting from either a middle–index response ($z = 3.32, p < .01$) or single-digit response ($z = 4.47, p < .01$) to a thumb–index response occurred significantly more often than the opposite pattern of shifting in grip morphology. There was no significant difference in the occurrence of shifts from middle–index to single-digit responses compared with the opposite pattern ($z = -1.74, ns$).

Correlates between error rates, hand use, and age—Pearson product–moment correlations were performed between age and both error measures and the handedness indexes

of each error measure. No significant associations were found. Thus, no associations were found between age and overall gripping accuracy and hand use.

The relation between hand preference and hand skill—Lastly, the data from Experiment 1 were used to classify subjects as either left-handed, ambiguously handed, or right-handed, and the within-hand performances were compared in each group. The data from Experiment 1 were used because the largest number of observations were available for classification of subjects on the basis of hand preference. On the basis of the data from Experiment 1, there were 23 left-handed, 53 ambiguously handed, and 54 right-handed subjects. Paired t tests indicate that the total number of errors produced by the left hand were significantly higher than for the right hand in right-handed subjects, $t(53) = 3.03$, $p < .05$, and ambiguously handed subjects, $t(52) = 2.45$, $p < .05$. No significant differences in error rates between the left and right hand were found for left-handed subjects, $t(22) = 1.17$, ns . The mean number of total errors made by left-, ambiguously, and right-handed subjects are shown in Table 5.

General Discussion

The results from Experiment 3 indicate that chimpanzees made more errors in grasping small food items with the left compared with the right hand. In addition, thumb–index responses were the more effective grip morphology, and the chimpanzees were more likely to switch from either a single-digit or middle–index grip to a thumb–index grip than the opposite condition. Taken together, the results suggest that grip morphology, hand skill, and cerebral dominance for motor skill are related to each other in chimpanzees.

In terms of lateralized hand use, the collective data from the three experiments indicate that greater right hand use is associated with the use of a thumb–index grip. Moreover, performance differences are evident between the hands with more errors produced by the left compared with the right hand (see Experiment 3). This was particularly the case for right- and ambiguously handed subjects but not left-handed subjects. The evidence of differences in motor skill between subjects of different hand-preference classifications indicates that hand preferences in chimpanzees likely reflect differences in the abilities of the two hands for a given task. In other words, hand preference reflects hand skill, although that relationship is not perfect. In light of the fact that there were significantly more right-handed and ambiguously handed chimpanzees than left-handed chimpanzees (see Experiment 1), the results suggest that the differences in distributions of hand use reflect differences in hand skill. This is the first evidence of an association between hand preference and hand skill in chimpanzees. This is also the first evidence of a left hemisphere specialization for motor skill in chimpanzees.

The results of this study also demonstrate that the use of the thumb and index finger for grasping is a more efficient means of obtaining small food items from a flat, smooth surface (see Experiment 3) than other grip types observed within the context of these studies. This conclusion is supported by the findings that accuracy was better for thumb–index responses and that subjects were more likely to switch from either a middle–index or single-digit response to a thumb–index response than the opposite condition. There have been very few studies that have examined the influence of object size on accuracy for use of different grips in nonhuman primates. However, the results from this study are consistent with at least one other report (Jones-Engel & Bard, 1996). Jones-Engel and Bard reported that 13 juvenile chimpanzees used precision grips (defined as those using the thumb and index finger) more often when grasping smaller compared with larger foods. Welles (1976) has also reported that the use of precision grips increases as object size decreases in Old World monkeys and great apes but not in New World monkeys.

The association between grip morphology and hand use has the potential for explaining variation in the observed patterns of hand use for simple reaching in nonhuman primates, particularly when subjects are required to reach from either a bipedal or tripodal posture. There have been a number of studies that have shown that posture influences hand use with increased preferential use of the right hand or left hand, depending on the species, when subjects are required to reach from a bipedal compared with a quadrupedal posture (see Westergaard, Kuhn, & Suomi, 1998, for a review). For example, in prosimians that do not have well developed precision grips, such as lemurs and bushbabies or lesser apes such as gibbons, preferential use of the left hand is found when reaching from a bipedal compared with a tripodal posture (Olson, Ellis, & Nadler, 1990; Stafford, Milliken, & Ward, 1990; Ward, Milliken, Dodson, Stafford, & Wallace, 1990; Ward, Milliken, & Stafford, 1993). In contrast, in capuchin monkeys, chimpanzees, orangutans, bonobos, and gorillas, right-hand use in reaching increases when reaching from a bipedal contrasted with a tripodal posture (Hopkins, 1993; Hopkins, Bennett, Bales, Lee, & Ward, 1993; Olson et al., 1990; Spinozzi & Truppa, 1999). One potential explanation for the shifts toward preferential use of the right hand in great apes and capuchin monkeys is that their grip preference changes when reaching from a bipedal compared with a tripodal posture. This is likely the case because the orientation of the hand changes when reaching from a bipedal posture such that the palm of the hand faces down, perhaps facilitating the use of a thumb–index response. In contrast, when reaching from a tripodal posture, the orientation of the hand is the opposite with the palm facing upward, and this may facilitate the use of other types of grips. The influence of posture and other factors on grip morphology and hand use warrants further investigation.

The results on grip morphology and hand use also have implications for evolutionary models of human handedness. There has been much speculation on the evolution of handedness in relation to emergent human characteristics such as tool use, language, and bipedalism (see Bradshaw & Rogers, 1993, for a review). However, recent studies in many vertebrates have reported population-level asymmetries, and some of these have examined motor functions associated with limb use (see Bisazza, Rogers, & Vallortigara, 1998, for a review). For example, some species of toads have been reported to show right-limb preferences in the removal of adhesive tape from the head, whereas others have shown a right-limb bias when reorienting themselves from a supine to prone posture when submerged in water (Bisazza, Cantalupo, Robins, Rogers, & Vallortigara, 1996, 1997). Although mice were initially thought to be bimodally distributed in paw preference, at least one recent study has shown that mice can exhibit population-level limb preferences for different tasks (Waters & Denenberg, 1994). In all of these studies, the effects have not been as robust as the degree of laterality reported in humans for handedness and have been more similar to those seen in great apes (and possibly other primates). Thus, right-sided asymmetries in motor functions may be a very basic attribute of the vertebrate central nervous system rather than having their origins in Hominid evolution (Vallortigara, Rogers, & Bisazza, 1999).

The relatively robust findings of population-level asymmetries in “lower” vertebrates need to be juxtaposed to the apparent difficulty in finding population-level asymmetries in “higher” vertebrates, such as nonhuman primates. There is no consensus that nonhuman primates exhibit population-level handedness (see McGrew & Marchant, 1997; Hopkins, 1999b, for contrasting views), and one would expect to find some consistency in findings between primate species if motor asymmetries are homologous between species representing a wide range of vertebrates. As previously noted, one problem has been the lack of common measures and procedures for assessing hand use in different species, and this may explain the lack of consistency in findings. Alternatively, asymmetries in motor function may have evolved multiple times in vertebrate evolution, and therefore the types of asymmetries seen in lower vertebrates may not have any origin to those seen in humans. The only way to resolve this issue is to test a wider range of nonhuman primate species using common measures and procedures for evaluating hand use.

What is unclear from this series of experiments is whether the differences in performance between the left and right hands are derived from practice or whether the preferences are derived from inherent differences in motor skill between the left and right hemispheres. Previous studies have reported that chimpanzees' hand preference is heritable, even among related individuals reared in separate environments (Hopkins, 1999a; Hopkins, Dahl, & Pilcher, 2001). There is also evidence of population-level right-ward asymmetries in neonatal chimpanzees for head turning (Hopkins & Bard, 1995), hand-to-mouth behavior (Hopkins & Bard, 1993), leading limb in locomotion (Hopkins, Bard, & Griner, 1997) and reflexive grasping of the hands and feet (Fagot & Bard, 1995). Taken together, these results suggest that asymmetries are present early in life and are possibly under genetic control, suggesting that inherent asymmetries in motor skill underlie the development of hand preferences in grasping. However, practice effects cannot be ruled out because the measure of hand preference and skill used in this study was not novel to the apes. Further research is needed to test these different interpretations of the results.

In Experiment 1, age was negatively correlated with grip morphology. Younger subjects were more inclined to adopt a thumb-index response than older subjects. Whether this association is due to decreased skill in older subjects is not clear. There was no association between age and grasping performance in Experiment 3; therefore, it does not appear that older subjects had any more difficulty in grasping the objects than younger subjects. Thus, it may be that older subjects adopt different gripping styles compared with younger individuals.

A sex difference in grasping was found in Experiment 3. Males performed worse than females for both measures of grasping accuracy. One explanation for the difference may be that females exhibit better fine motor skill than males, a result consistent with some reports in humans (Kimura, 1999). Alternatively, males have larger hands than females and, all things being equal, it was more difficult for their larger hands to grasp the small peanuts than the females. As a means of potentially determining the effect of hand size on sex differences in error rates, we determined the body weight of each subject from the animal records at the YRPRC. We used the last recorded body weight for each individual that was recorded in the animal records file, and all of the weights were taken within 1 year of the onset of this study. An analysis of covariance was performed, with the two error measures serving as the dependent measures. Sex was the independent variable, while age and body weight were the covariates. For both error measures, no significant effect for sex was found, although both F values approached conventional levels of statistical significance ($p = .1$). The average number of errors for males and females were 12.94 ($SD = .59$) and 10.82 ($SD = .49$), respectively. Thus, the size of the hand (as estimated from body weight) does appear to mediate error rates in simple reaching, but it does not entirely explain all the variation in performance. Ideally, measuring the grasping of objects that are scaled to the size of the hands would be necessary to determine which of these two explanations is more plausible.

In conclusion, the results of this study indicate that increased right-hand use in grasping is associated with the use of a thumb-index grip in chimpanzees. Both between- and within-subject variability in hand use is associated with variation in grip morphology. The results further indicate that performance in grasping small pieces of food is performed significantly better by the right compared with the left hand, particularly among right- and ambiguously handed subjects. These results suggest that the left hemisphere is specialized for motor skill in chimpanzees and that hand preferences likely reflect inherent biases in skill. Whether the observed functional asymmetries in motor skill are associated with asymmetries in neuroanatomical areas controlling motor function remain unknown. However, great apes show a left-hemisphere asymmetry in a portion of the precentral gyrus that is associated with individual digit control of the fingers (Hopkins & Pilcher, 2001), and it is possible that asymmetries in this region will correlate with functional asymmetries in hand skill. This

hypothesis awaits further investigation, but with the recent use of noninvasive imaging techniques in nonhuman primates (e.g., Hopkins, Marino, Rilling, & MacGregor, 1998; Rilling & Insel, 1999), testing for an association between functional and structural asymmetries in nonhuman primates seems feasible in the not too distant future. These studies will shed important light on the evolution of brain and behavior relationships in primates, including humans.

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Figure 1.
Mean handedness index as a function of hand preference classification.

Figure 2.

Mean handedness index for thumb–index and middle–index responses in the chimpanzees studied by Tonooka and Matsuzawa (1995) and the chimpanzees in this study. The data on the right side are from “Hand Preferences in Captive Chimpanzees (*Pan troglodytes*) in Simple Reaching for Food,” by R. Tonooka & T. Matsuzawa, 1995, *International Journal of Primatology*, 16, p. 20. Copyright 1995 by Kluwer Academic. Adapted with permission.

Figure 3.
Mean number of responses for the left and right hand as a function of food type.

Figure 4.
Mean number of errors for the left and right hand.

Figure 5.
Mean percentage of errors as a function of grip type.

Table 1
Mean Proportion of Grip Types for Males and Females (Experiment 1)

Sex	Grip type		
	Thumb index	Middle index	Single digit
Male	.63	.34	.03
Female	.45	.54	.01

Table 2

Mean Number of Responses (and Standard Errors) for Each Grip Type as a Function of Food Type (Experiment 2)

Food type	Grip type		
	Thumb index	Middle index	Single digit
Peanuts	15.82 (0.84)	7.29 (0.83)	1.97 (0.38)
Raisins	13.71 (0.91)	10.67 (0.91)	0.66 (0.22)

Table 3

Mean Error Rates (and Standard Errors) for Each Measure as a Function of Sex (Experiment 3)

Sex	No. of trials	Total errors
Male	6.73 (0.39)	10.36 (0.71)
Female	5.21 (0.35)	7.89 (0.65)

Table 4
Distribution of Shifting Responses as a Function of Grip Type (Experiment 3)

Shift in grip	Hand		Total
	Left	Right	
Thumb index → middle index	11	5	16
Middle index → thumb index	23	18	41
Thumb index → single digit	13	7	20
Single digit → thumb index	28	32	60
Single digit → middle index	13	5	18
Middle index → single digit	9	2	11

Table 5

Mean Number of Total Errors (and Standard Errors) Made by Left-, Ambiguously, and Right-Handed Subjects (Experiment 3)

Hand preference	Left hand	Right hand
Left-handed	10.47 (1.73)	8.52 (1.11)
Ambiguously handed	10.71 (1.06)	8.41 (0.78)
Right-handed	9.43 (0.83)	6.85 (0.76)