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Note

Further evidence of a right hand advantage in motor skill by chimpanzees (*Pan troglodytes*)

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Abstract

Asymmetries in motor skill when grasping small food items was evaluated in a sample of captive chimpanzees. In two experiments, error rates in grasping food were assessed when controlling for individual differences in grip morphology. In both experiments, chimpanzees were found to make more errors with the left compared to the right hand. Male chimpanzees were also found to make more errors compared to females. These results are discussed in the context of a presumed disassociation between hand preference and performance as indicators of cerebral dominance in motor functions.

Keywords: Manual skill; Chimpanzees; Handedness; Grip morphology

1. Introduction

A significant majority of human subjects, across many different cultures, self-report themselves as being right-handed (Annett, 1985; Porac & Coren, 1981). Right hand preferences are often interpreted as an indicator of the left hemisphere's dominance for motor skill; however, a number of studies in human subjects have shown that the magnitude and distribution of asymmetries in motor skill are somewhat different than asymmetries in self-reported hand preference per se (Annett, 1992; McManus, Murray, Doyle, & Baron-Cohen, 1992; Napier, 1960; Peters, Servoas, & Day, 1990). For example, the percentage of concordance between performance and preference measures of handedness vary between 59 and 85%, respectively (Porac & Coren, 1981). Asymmetries in motor skill are skewed to the right, but generally assume a normal distribution. In contrast, hand preference distributions are J-shaped and are more pronounced on the tail indicating right handedness. This has led some to suggest that asymmetries in motor skill are somewhat independent of asymmetries in hand preference per se (Porac & Coren, 1981). Alternatively, the differences in hand preference and performance distribution may inherently reflect the different scales of measurement (questionnaire versus behavioral data) used to evaluate each dimension of handedness.

Recent studies in non-human primates and other vertebrates have demonstrated evidence of population-level asymmetries in hand or limb preferences (Bisazza, Rogers, & Vallortigara, 1998; Bradshaw & Rogers, 1993; Hook-Costigan & Rogers, 1997; Hopkins, 1999; MacNeilage & Studdert-Kennedy, 1987; Marchant & McGrew, 1991; McGrew & Marchant, 1997; Rogers & Andrews, 2002). However, less clear from the existing studies is whether hand (or limb) preferences infer any advantages in motor skill for the left- and right hands. In fact, there are very few studies that have examined asymmetries in motor skill in non-human animals, notably primates (Butler, Stafford, & Ward, 1995; Fragaszy & Adams-Curtis, 1993; Hopkins, Washburn, & Rumbaugh, 1989; Lacreuse & Fragaszy, 1997; McGrew, Marchant, Wrangham, & Klein, 1999; Peters, 1991; Preilowski, 1993; Welles, 1976). Andrews and colleagues (Andrews & Rosenblum, 1994, 2001) have assessed acquisition rates on a psychomotor task, in which subjects had to learn to control a cursor displayed on a computer monitor, in socially-housed macaques and found no significant differences in acquisition rates between subjects trained with the left or right hand. Moreover, Andrews and Rosenblum (1994,

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2001) found no link between performance on the psychomotor tasks and subsequent preferences for use of the joystick. In contrast, Hopkins, Washburn, Berke, and Williams (1992) found that rhesus monkeys that preferred to use their right hand acquired the same psychomotor task significantly faster than subjects that preferred to use their left hand. In these two studies, the task was fairly complex and involved much more than motor functions associated exclusively with the hand. Other investigations of motor skill have focused more specifically on performance differences between the left- and right hand when grasping for various sized food objects. For example, Rigamonti, Previde, Poli, Marchant, and McGrew (1998) recorded the hand use, response latency and error rate in grasping small pellets in a sample of 10 macaques. In terms of performance differences, the preferred hand made fewer errors and responded more quickly than the non-preferred hand. No direct comparison between the left- and right hand was made, but six subjects preferred the right hand while three preferred the left (one had no preference). Interestingly, on successful reaching responses, the subjects were faster with the left compared to the right hand, irrespective of whether they preferred the right or left hand. The evidence of faster response times for the left hand is consistent with recent findings in rhesus monkeys that were required to remove small candies from differently shaped wire patterns (Lacreuse & Herndon, 2003). Likewise, it has been reported that infant chimpanzees ($n = 13$) grasp small objects using an imprecise grip faster with the left compared to the right hand. In contrast, power grips were executed faster with the right compared to the left hand in this same sample of 13 captive chimpanzees (Jones-Engel & Bard, 1996).

One problem with many of the previous studies on laterality and motor skill in monkeys and apes is that sample sizes have been relatively small and variation in different grip preferences have not been controlled for between individuals. Recently, Hopkins, Cantalupo, Wesley, Hostetter, and Pilcher (2002) addressed the issue of sample size by examining error rates of the left- and right hand in grasping small food items in a sample of 140 chimpanzees. Hopkins et al. (2002) required chimpanzees to grasp small food items and 20 trials were presented to the left- and right hands. Overall, subjects made fewer errors with the right compared to the left hand and this pattern of results was more pronounced in subjects classified as right-handed compared to left- and ambiguously-handed subjects. Additional analyses indicated that chimpanzees made fewer errors when using the thumb and index finger for grasping compared to subjects that grasped the food items using less precision type grasps. One limitation of the Hopkins et al. (2002) was that grip morphology varied between subjects and hands. Indeed, some subjects used exclusively a thumb–index grasping response, others used exclusively a middle–index finger grasping response and still other used different grasping responses between the left- and right hand. Because error rates differed as a function of grip type, it was not clear whether the evidence of lower error rates in the right compared to the left hand were an artifact of differential use of grip morphology between hands and across subjects.

The purpose of this study was to further examine performance differences in grasping small food items in chimpanzees while explicitly controlling for grip morphology across subjects and between hands. Two experiments were conducted: In Experiment 1, error rates of the left- and right hand were compared in chimpanzees when adopting the same grasping morphology. In Experiment 2, individual preferences in grasping morphology were identified in the sample of chimpanzees. Error rates between the left- and right hands were then compared when subjects used their preferred grip type rather than comparing subjects using the same grasping morphology. If the right hand is more skilled than the left hand, as previously reported by Hopkins et al. (2002), then significantly fewer errors should be made for the right compared to the left hand.

2. Method

2.1. Subjects

In the initial experiment, there were 113 captive chimpanzee subjects housed at the Yerkes National Primate Research Center of Emory University. There were 68 females and 45 males and the subjects ranged in age from 3 to 47 years of age, respectively. With the males, there were 19 mother-reared and 26 human-reared individuals. Within the females, there were 43 mother-reared and 25 human-reared individuals. Human-reared subjects were chimpanzees that entered a nursery prior to 30 days of life and were taken care of by humans (Bard, 1996). Mother-reared subjects were individuals that stayed with their conspecific mother beyond 30 days of life.

2.2. Materials

Error rates in grasping were assessed for three different foods including stick pretzels, M&M minis, and Tart n' Tiny candies. The pretzels were 60 mm long and 4 mm in diameter. The M&Ms measured 9 mm in diameter and were approximately 3.5 mm thick. The Tart n' Tinys measured 8 mm × 6 mm and were cylindrical in shape with rounded edges and a hard smooth coating.

2.3. Procedure

The experiment was conducted in the focal subjects' home cages. Subjects housed at the YNPRC Main Center were tested in the outdoor portion of their home cages which measured 6 m × 3 m × 3 m and were constructed with concrete flooring. Subjects housed at the YNPRC Field Station were tested in the indoor portion of their home cages to ensure a comparable flooring surface since the outdoor portion of their cages consisted of natural dirt, grass, and bark. The inside portions of the Field Station subjects' home cages were comparable in size to the outdoor Main Center cages.

The goal of the current experiment was to assess error rates when all subjects had to use the most commonly used grip type, that being the thumb–index grasp. Thumb–index gripping was recorded when the subjects abducted the thumb to the lateral or tip of the index finger to grip the food item. Not all subjects exclusively used thumb–index responses and we recorded the occurrences of other grips types used while testing; however, we did not record whether the subjects made an error or not when grasping the food items because we were specifically interested only in the error rates when the subjects used a thumb–index grip. The number of errors made when making 10 thumb–index responses was recorded for the left- and right hand for all subjects and for each food type. An error was defined as any failed attempt at grasping the food item in which the subject either had to re-grip the food item in order to pick it up or the subject dropped the food item and had to pick it up again in order to bring it to his mouth. The food items were presented in random order with no specific emphasis on counterbalancing the presentation order. However, subjects finished testing on one food item before being tested on a different food.

At the onset of each trial, the experimenter would throw the target food into the focal subject's home cage and record the hand used, grip type, and how many errors they made, if they used a thumb–index grip type. Both right and left hand responses were recorded until 10 pieces of food had successfully been picked up and consumed using a thumb–index grip by each hand. The frequency of occurrence of other grip types, notably the use of the middle–index finger grip was also recorded as this is the next most commonly used grip type. The thumb–index and middle–index grasping responses make up over 95% of the grips used in this colony of chimpanzees (see Hopkins et al., 2002).

Note that if a subject was reluctant to use one hand over the other, the experimenter would intentionally throw the food items into the cage in a location that would encourage the subject to use the non-dominant hand. In a few cases in which the subject did not prefer the thumb–index grip, it was necessary to throw the food items in a location that would require the chimpanzee to move into a position in which thumb–index gripping is more likely to occur (usually tripedal, reaching behind the plane of the shoulders). In this way it was assured that 10 thumb–index responses were recorded for both the left- and right hands for each subject.

2.4. Data analysis

At the end of data collection, the number of errors made by each hand was averaged across the three food types and this served as the primary measure of interest. The average number of middle–index responses made in the process of collecting the 10 thumb–index responses was also calculated and served as a covariate in subsequent analyses. The data were analyzed using parametric-statistics and alpha was set to $P < 0.05$. All post-hoc tests were performed using Tukey's Honestly Significant Difference test (HSD).

3. Results

3.1. General descriptive information

Shown in Table 1 are the average number of errors made and the average number of middle–index responses produced for males and females. Two independent samples *t*-tests comparing males and females on each of these general aspects of performance failed to reveal significant differences, once adjusting alpha for the number of tests performed. Sex differences did approach conventional levels of significance for the overall error rates with males making more errors than females (see Table 2). To further exploit the potential sex difference found in error rates, a series of independent samples *t*-tests were run comparing the error rates of males and females for each food type. These results are shown in Table 2. For two of the three foods, the females performed better than the males. Pearson Product Moment correlations revealed consistency between error rates and the production of middle–index finger responses between the different food types used in this study, as shown in Table 3. All correlation coefficients between the three food types were

Table 1
Mean number of errors and middle–index responses in male and female chimpanzees

Sex	Overall error rate	Middle–index responses
Females	1.65	5.85
Males	2.27	5.14
t	2.04	0.49
P	0.044	0.621

Table 2
Mean number of errors (and standard errors) as a function of food type and sex

Food type	Males (S.D.)	Females (S.D.)	*t*	*P*
Pretzels	3.50 (0.598)	2.33 (0.295)	−1.94	0.055
M&Ms	1.31 (0.232)	1.33 (0.181)	0.058	0.954
Tart n' Tinys	2.54 (0.376)	1.62 (0.174)	−2.44	0.016
Overall mean	1.65 (0.150)	2.27 (0.290)	−1.89	0.062

Table 3
Intercorrelations in the number of errors and number of middle–index responses between the three different food types

Food type	Number of errors	Middle–index responses
Pretzel + M&M	0.262	0.715
Pretzel + Tiny n' Tart	0.393	0.635
M&M + Tiny n' Tart	0.352	0.705

All correlations were significant at $P < 0.05$.

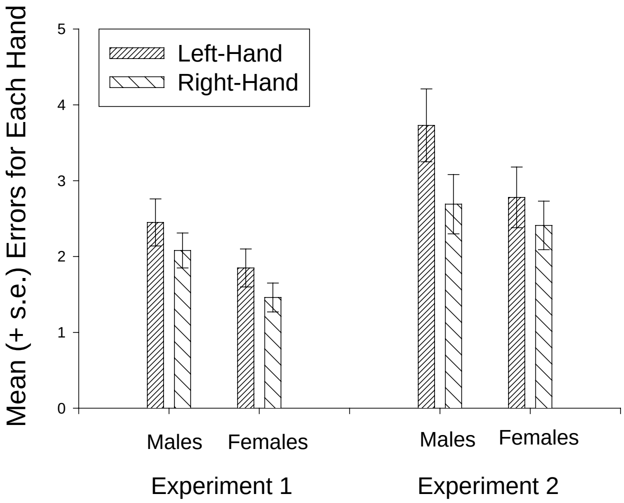

Fig. 1. Mean number of errors made by males and females for the left- and right hand in Experiments 1 and 2.

significant at $P < 0.01$. Thus, at the individual level, the chimpanzees were consistent in their grasping errors and their use of middle–index finger grip.

3.2. Laterality effects

For this analysis, a mixed model analysis of covariance (ANCOVA) was used. The repeated measures variable was hand use (left, right) while the between group variables were sex (male, female) and rearing history (mother-reared, human-reared). The covariate was the number of middle–index responses for each hand. The ANCOVA revealed significant main effects for hand $F(1.107) = 4.55$, $P < 0.01$ and sex $F(1.107) = 4.16$, $P < 0.04$. Shown in Fig. 1 is the mean number of errors for each hand as a function of sex. Overall, the chimpanzees made significantly more errors with the left compared to the right hand. Male chimpanzees made significantly more errors than females.

4. Discussion, Experiment 1

The results of Experiment 1 were relatively straightforward. First, overall error rates were consistent across food types. Second, males made more errors than females. Third, the chimpanzees made significantly more errors with the left compared to the right hand.

The evidence of better performance by the right compared to the left hand is consistent with the previous findings by Hopkins et al. (2002) and more importantly, these results cannot be attributed to individual differences in the grip morphology adopted by the subjects. Thus, the findings strengthen the interpretation that the right hand (and therefore the left hemisphere) is specialized for motor skill. One problem with this experiment is that some subjects never adopted or were extremely resistant to using a thumb–index response and therefore were not included in the experiment. Therefore, arguably there is a sampling bias in our chimpanzees with the selective inclusion of subjects that used thumb–index responses more frequently. To address this issue, a second experiment was conducted. In Experiment 2, rather than have all subjects adopt the same grip, individual differences in grip morphology preferences were determined for each subject. Differences in error rates in grasping were then compared between the left- and right hands based on the preferred grip of each subject and hand.

5. Methods, Experiment 2

5.1. Subjects

Subjects were 137 captive chimpanzees (*Pan troglodytes*) housed at the Yerkes National Primate Research Center (YNPRC) of Emory University, ranging in age from 4 to 48 years ($m = 20.04$ years). Of the 137 subjects, 81 were females and 56 were males.

5.2. Procedure

The subjects were tested in the same housing conditions as in Experiment 1. Before beginning the experiment, subjects were classified by their gripping preference for each hand as either (a) thumb–index graspers, (b) middle–index graspers or (c) non-preferred graspers based on previous published data (Hopkins et al., 2002). In the Hopkins et al. (2002) paper, hand preference and grip morphology was recorded when grasping 25 shelled peanut halves. The total number of thumb–index responses for each hand was divided by the total number of responses for that hand in order to calculate the proportion of responses for each hand that were thumb–index responses. Since thumb–index and middle–index grasps make up over 95% of responses made in this colony of chimpanzees (see Hopkins et al., 2002), non-thumb–index responses were assumed to be middle–index responses for the purpose of grip preference classification. Subjects who used a thumb–index grip on 33% or less of their overall responses for a given hand were classified as middle–index graspers. Subjects who used a thumb–index grip more than 33% but less than 66% of the overall responses for a given hand were categorized as non-preferred graspers for that hand. Subjects who responded with a thumb–index grasp 66% or more of the overall responses for a given hand were classified as thumb–index graspers for that hand. In this way, a gripping preference was established for both the left- and right hand of each subject.

Using the above described gripping preference classifications, the experimenter recorded error rates for the preferred grip type for each hand. For each subject, the experimenter would throw shelled peanut halves, one at a time, into the focal subject's home cage and record errors made with each hand using the preferred grasp. Errors in grasping were defined in the same way as that used in Experiment 1. In cases in which one hand was classified as a non-preferred grasp and the other hand with a preference, the experimenter attempted to collect data on the same grip type for the non-preferred grasping hand as the hand with a preference. For example, if the left hand was classified as having no grasping preference and the right hand was classified as a thumb–index grasper, then the experimenter attempted to record thumb–index responses for both hands. In cases in which there was no grip type preference for either hand, the experimenter recorded all responses until ten responses were recorded for one grip type for each hand independently. As with Experiment 1, if a subject was reluctant to use one hand over the other, the experimenter would intentionally throw the peanut halves into the cage in a location that would encourage the subject to use the less dominant hand. In this way, the error rates were recorded for 10 responses with each hand.

6. Results

6.1. Descriptive information

Of the 137 subjects tested, the number of subjects classified as thumb–index graspers for both hands, middle–index graspers for both hands, or mixed-preferent graspers (one hand preferred one grip and the opposite hand preferred a different grip) was not randomly distributed as determined by a chi-square goodness-of-fit test $\chi^2(2, N = 137) = 62.77$, $P < 0.001$. The number of thumb–index, middle–index and mixed-preferent individuals was 89, 29, and 19, respectively. Within the mixed-preferent group, there were nine subjects that preferred to use a thumb–index response for their left hand and a middle–index response for their right hand. In contrast, there were 10 mixed-preferent chimpanzees that preferred to use a thumb–index response for their right hand and a middle–index response for their left hand. Chi-square tests of independence revealed a significant association between rearing history and grip preference but not between sex and grip preference. These distributions can be seen in Table 4. As can be seen, there were more middle–index and fewer thumb–index classified subjects in the mother- compared to human-reared chimpanzees. Pearson product moment correlations failed to reveal any significant associations between age and either hand preference or the total number of errors in grasping.

Table 4
Distribution of grip preferences as a function of rearing history and sex

	Grip preferences		
	Thumb–index	Middle–index	Mixed
Rearing history			
Mother-reared	36	20	14
Human-reared	53	9	5
Sex			
Males	36	9	11
Females	53	20	8

6.2. Grip preference, hand use and error rates

For the initial analysis, a mixed-model analysis of variance was performed. Hand use was the repeated measure (left, right) while grip preference (thumb–index, middle–index, mixed-preferent) and rearing history (mother, human) served as between group variables. This analysis revealed significant main effects for hand use $F(1, 131) = 5.85$, $P < 0.001$, rearing history $F(1, 131) = 5.59$, $P < 0.001$ and grip preference $F(2, 131) = 4.71$, $P < 0.001$. There were no significant two- or three-way interactions. Subjects made significantly more errors with the left (mean = 3.99) compared to the right (mean = 3.07) hand and mother-reared subjects (mean = 2.77) made significantly fewer errors than human-reared (mean = 4.29) subjects (see Fig. 1). Lastly, post-hoc analysis indicated that thumb–index preferent (mean = 2.45) subjects made significantly fewer errors than mixed-preferent (mean = 4.71) subjects but not middle–index preferent subjects (mean = 3.43).

Because there was such a large discrepancy in the number of individuals classified as thumb–index, middle–index and mixed-preferent and this variable was associated with rearing history, a second analysis was performed in which the effect of grip preference was evaluated using a matched design. Specifically, for all 29 subjects classified as middle–index preferent, we matched them with a thumb–index preferent chimpanzee that had the same sex, age (within 1 year) and rearing history (mother, human). Mixed-preferent subjects were eliminated from this analysis. The error rates of the left- and right hand between the two groups of chimpanzees were compared using a repeated measures ANOVA with hand (left, right) serving as the repeated measure and grip preference (thumb–index, middle–index) serving as the between group variable. This analysis revealed a significant main effect for hand use $F(1, 56) = 5.52$, $P < 0.01$. Subjects made significantly more errors with the left compared to the right hand. No other significant main effects or interactions were found.

7. General discussion

The results of Experiment 2 were straightforward. As with Experiment 1, the chimpanzees showed a right hand advantage in motor skill, as reflected in the number of errors made when grasping a small food item. This effect could not be explained on the basis of individual differences in grip morphology, since each subject was tested using their preferred grip. Thus, the collective data between Experiments 1 and 2 strongly suggest that captive chimpanzees show right hand advantages in motor grasping, a finding consistent with previous studies (Hopkins et al., 2002).

No significant difference in error rates were found between subjects that adopted different grip preferences. In other words, subjects that preferred to use a thumb–index grip made as many errors as subjects that preferred to use a middle–index grip. This was somewhat surprising in light of the fact that there has been such evolutionary selection toward the use of the thumb for grasping in non-human primates (see Marzke, 1997). If adopting a thumb–index grasp confers some advantage in grasping small objects in non-human primates, the methods used in this study were not sensitive enough to detect those differences. It should be emphasized that the statistical majority of the chimpanzees did adopt a thumb–index response, and therefore, the representation of this grasping strategy was pronounced but it did not translate into more efficient performance. Testing chimpanzees that use different grip morphologies on more sophisticated behavioral measures of motor skill, such as tool use, might reveal performance differences related to motor skill (e.g., Boesch & Bosech, 1993).

Sex differences in error rates for grasping were also evident in both Experiments 1 and 2 with males making more errors than females. This result is consistent with previous studies on grasping in chimpanzees (Hopkins et al., 2002) but should be interpreted with some caution because there are morphological differences in the size of the hand that are confounded with sex (Provins, 1997). Males have larger hands and therefore the objects used for grasping are relatively smaller for them compared to females. Whether sex differences are evident in chimpanzees will require more controlled experiments in which the size of the object is controlled relative to the size of the hand.

In conclusion, the findings from these two experiments indicate that chimpanzees make fewer errors with the right compared to the left hand when grasping small food items. These results cannot be attributed to individual differences in grip morphology and therefore strongly suggest a left hemisphere advantage in motor skill. The results are also different from previous studies on asymmetries in motor skill in monkeys in that the chimpanzees show a right rather than left hand advantage in motor skill (e.g., Lacreuse & Herndon, 2003). Recent neuroanatomical studies in non-human primates have revealed significant population-level asymmetries in several brain areas associated with handedness in humans including the planum temporale (Gannon, Holloway, Broadfield, & Braun, 1998; Hopkins, Marino, Rilling, & MacGregor, 1998), Brodmann's area 44 (Cantalupo & Hopkins, 2001), and the motor-hand area within the precentral gyrus (Hopkins & Pilcher, 2001). Whether the asymmetries in motor skill reported here are linked with variation in cerebral morphology remains to be addressed but with the increasing use of non-invasive brain imaging technologies in non-human primates, these issues can be addressed in the not too distant future.

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