

Handedness influences intermanual transfer in chimpanzees (*Pan troglodytes*) but not rhesus monkeys (*Macaca mulatta*)

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Abstract Intermanual transfer refers to an effect, whereby training one hand to perform a motor task improves performance in the opposite untrained hand. We tested the hypothesis that handedness facilitates intermanual transfer in two nonhuman primate species: rhesus monkeys ($N = 13$) and chimpanzees ($N = 52$). Subjects were grouped into one of four conditions: (1) left-handers trained with the left (dominant) hand; (2) left-handers trained with the right (nondominant) hand; (3) right-handers trained with the left (nondominant) hand; and (4) right-handers trained with the right (dominant) hand. Intermanual transfer was measured using a task where subjects removed a Life Savers[®] candy (monkeys) or a washer (chimpanzees) from metal shapes. Transfer was measured with latency by

comparing the average time taken to solve the task in the first session with the trained hand compared to the first session with the untrained hand. Hypotheses and predictions were derived from three models of transfer: *access*: benefit training with nondominant hand; *proficiency*: benefit training with dominant hand; and *cross-activation*: benefit irrespective of trained hand. Intermanual transfer (i.e., shorter latency in untrained hand) occurred regardless of whether monkeys trained with the dominant hand or nondominant hand, supporting the *cross-activation* model. However, transfer was only observed in chimpanzees that trained with the dominant hand. When handedness groups were examined separately, the transfer effect was only significant for right-handed chimpanzees, partially supporting the *proficiency* model. Findings may be related to neurophysiological differences in motor control as well as differences in handedness patterning between rhesus monkeys and chimpanzees.

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Introduction

There is increasing interest in understanding the role of lateralization in the primate motor system, particularly with regard to the evolution of hemispheric specialization and the sharing of motor information between hemispheres (e.g., Mutha et al. 2013). The motor system is comprised of pathways from the cerebral cortex and the brain stem to the cortical spinal fibers and motoneurons, which innervate movements of the opposite side of the body and limbs (Kuypers 1982). This asymmetrical movement control is thought to contribute to asymmetries observed in

behavior—most notably the phenomenon of handedness (Hammond 2002). The prevalence of right-handedness in humans is typically reported as 90 % (e.g., Annett 2002). Though it has been known for quite some time that individual monkeys and apes show hand preferences for certain tasks, whether they exhibit population- or species-level handedness remains an area of interest and debate (for reviews and discussion, see MacNeilage et al. 1987; MacNeilage 2007; Marchant and McGrew 2013; McGrew and Marchant 1997; Meguerditchian et al. 2013; Papademetriou et al. 2005). In this study, we sought to compare performance for learning a novel motor task in two non-human primate species: rhesus monkeys (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*). These species were selected because (1) they differ in the motor control of the arms and (2) they differ with respect to the direction and distribution of handedness, as described below.

Primates have been the focus of many motor control studies due to the extensive corticospinal fiber projections to the intermediate zone and ventral horn as compared to other animals. These corticospinal fibers strengthen motor control by linking to motoneurons, and they provide the capacity for highly selective voluntary movements in the finger and hands (Brinkman and Kuypers 1973). In rhesus monkeys, the corticospinal fibers connect directly to motoneurons (Nakajima et al. 2000) and are distributed to the dorsal, lateral, and central sections of the contralateral intermediate zone, which innervate muscles in the hands and feet (Kuypers 1982). Chimpanzees share similar direct cortical fiber connections and distribution, but the fiber connections to the motoneurons occur in greater quantities and innervate muscles in the distal extremities as well as proximal muscles closer to the trunk of the body (Kuypers 1982). Moreover, hand, finger, and upper arm movements are controlled ipsilaterally in rhesus monkeys (Brinkman and Kuypers 1973). Similar to humans, but unlike rhesus monkeys, chimpanzees have limited ipsilateral control of the arm; rather, the contralateral hemisphere controls the majority of each arm (Kuypers 1982).

Chimpanzees and rhesus monkeys also differ with respect to handedness. There is substantial evidence for population-level right-handedness in chimpanzees (e.g., Hopkins 1995, 2006; Hopkins et al. 2004, 2011; Llorente et al. 2011; Wesley et al. 2002). The rightward bias in chimpanzees is similar to that of humans, although the pattern is not as robust, with a ratio of 2:1 right in chimpanzees compared to 9:1 right in humans. By contrast, handedness findings in rhesus monkeys are equivocal due to inconsistent reports across studies. While some investigators have reported a population-level left preference in rhesus monkeys (e.g., Beck and Barton 1972; Westergaard et al. 1997), others have noted no population-level bias, although some monkeys expressed clear individual preferences (e.g.,

Bennett et al. 2008; Deuel and Dunlop 1980; Hopkins et al. 1992; Nelson et al. 2011). The differences in direction and distribution of handedness between chimpanzees and rhesus monkeys may be in part related to the differences in the control of arm and hand movements between the two species: Rhesus monkeys maintain some ipsilateral control, particularly for the upper arm, while chimpanzees rely largely on contralateral control.

Intermanual transfer between hemispheres (i.e., hands) is commonly investigated by learning a motor task with one hand and testing whether performance improves in the opposite untrained hand (Schulze et al. 2002). Multiple models for the mechanism of interhemispheric transfer have been discussed in the human literature. The callosal *access* model postulates that motor programs are stored in the dominant hemisphere irrespective of the hand used during training, and the corpus callosum is responsible for communicating these programs to the nondominant hand (Taylor and Heilman 1980). Thus, the dominant hand (DOM) has direct access to motor programs, whereas the nondominant hand (NDOM) only has indirect access. Therefore, this model predicts a unidirectional effect of transfer benefits in NDOM → DOM training because motor programs are stored in the dominant hemisphere, even when the NDOM hand is trained. A second model for transfer that implicates handedness is the *proficiency* model, which postulates that the untrained hand can use skills learned by the more proficient (DOM) hand (Ammons 1958; Laszlo et al. 1970; Parlow and Kinsbourne 1989). This model predicts the opposite direction of transfer benefits in which greater performance gains are seen in DOM → NDOM training. Under this model, motor engrams are stored in both hemispheres when the DOM is trained, yielding greater transfer to the untrained (NDOM) hand. Conversely, a single motor engram is stored in the nondominant hemisphere when the NDOM is trained, resulting in fewer transfer performance benefits.

A third model for transfer does not implicate handedness effects. The *cross-activation* model postulates that performing tasks with a single hand generates neural activity both contralateral and ipsilateral to the trained hand (Parlow and Kinsbourne 1989; Lee et al. 2010). This model predicts transfer in both directions (NDOM → DOM and DOM → NDOM). Motor engrams are stored in both hemispheres despite which hand is originally trained, always resulting in transfer performance benefits for the untrained hand. With these distinctions between intermanual transfer models in mind, it is possible that they share some overlap or may vary between tasks and experimental subgroups (see Parlow and Kinsbourne 1989). For example, some studies with humans have demonstrated that the DOM benefits more from NDOM training (e.g., Taylor and Heilman 1980), supporting the callosal *access* model, while other

studies have shown that the NDOM benefits more from DOM training (e.g., Halsband 1992; Laszlo et al. 1970), supporting the *proficiency* model.

One possibility for the conflicting reports in the literature regarding these three intermanual transfer models may be due to the variability in how investigators have quantified “transfer.” In prior analyses using a subset of the sample of chimpanzees reported on here, Phillips et al. (2013) computed a difference score of the total number of test sessions needed to reach a criterion between the trained and untrained hands on an intermanual transfer task. Greater performance improvements (i.e., larger difference scores) were found when chimpanzees trained with the NDOM and switched to the DOM, supporting the *access* model. In human work, Parlow and Kinsbourne (1989) demonstrated that the pattern of transfer is affected by which trials are used in analyses, with greater benefit in the opposite direction, DOM → NDOM, when early test trials are examined. They further argued that later test trials (i.e., trials meeting criterion) are confounded by same-hand training. One goal of the current study was to use average latency during first session task exposure to examine whether early trials provide different information about intermanual transfer than later trials (i.e., trials from final sessions when subjects reach a time criterion).

Although there are no prior studies in rhesus macaques, both time to criterion and latency have been used to quantify transfer in Japanese macaques. Obayashi et al. (2003) reported that Japanese macaques took 2 weeks on average to learn a tool-use task with the trained hand, as opposed to just a few days with the untrained hand. Although the authors noted whether training began with the left or right hand in this study, the monkeys’ hand preferences were not reported. In another study with Japanese macaques, monkeys practiced one set of a task with one hand and a separate set with the opposite hand; both hands were tested on each set after a delay of 18 months (Hikosaka et al. 2002). There was no difference in the number of errors made by either hand regardless of training. However, latency to solve the task was significantly shorter in the hand that had trained originally on the given set. Again, handedness was not analyzed in this study of motor learning, although a transfer effect was evident. Another goal of the current study was to examine whether handedness influences intermanual transfer in nonhuman primates, using predictions for transfer effects made by the *access*, *proficiency*, and *cross-activation* models.

The difference in patterns of hand use between chimpanzees and rhesus monkeys may indicate a difference in the relationship between lateralization and the organization of the motor system, particularly with regard to how information is transferred between hemispheres in each species. To address this question, we examined motor skill transfer in both

species on a task involving removing a Life Savers® candy (rhesus monkeys; experiment 1) or a metal washer (chimpanzees; experiment 2) from various metal rods (Bachevalier and Hagger 1991; Gash et al. 1999; Lacreuse et al. 2005; Lacreuse and Herndon 2003; Phillips et al. 2013; Smith et al. 1999; Zhang et al. 2000). We first conducted a baseline handedness assessment in both species to identify left- and right-handers. Following this assessment, we randomized subjects to start with either the DOM or the NDOM, thus creating four test groups in each species. Subjects were then trained with simple shapes on the rod task to ensure that they understood the goal of the task was to remove the candy or the washer (note: chimpanzees exchanged the washer for a food reward). Finally, the test of transfer was the average latency to solve the task in the first session with the trained hand compared to the first session with the untrained hand. We hypothesized that handedness would affect transfer in chimpanzees, but not rhesus monkeys, given the neurobehavioral differences between the species described previously. Therefore, we predicted that transfer patterns in monkeys would support the *cross-activation* model and transfer patterns in chimpanzees would support either the *access* or *proficiency* models. We did not predict the direction of greater transfer benefits in chimpanzees (NDOM → DOM vs. DOM → NDOM) because of the mixed literature in humans.

Experiment 1: monkeys

Methods

Subjects

Data were collected from 13 adult rhesus monkeys (*Macaca mulatta*) housed at the University of Massachusetts Amherst (eight males; five females). Monkeys ranged in age from 7 to 24 years. All monkeys were born in captivity. Five monkeys were individually housed in close proximity to other monkeys, and seven monkeys were socially housed with one or two other monkeys. Food and water were freely available throughout the experiment. The study was conducted in accordance with the Guide for Care and Use of Laboratory Animals and complied with the Animal Welfare Act. The University of Massachusetts Amherst Institutional Animal Care and Use Committee (IACUC) approved the research. All monkeys were tested individually in their home enclosures on the tasks.

Apparatus

The testing apparatus was constructed from a clear vertical Lexan panel (measuring 32 × 30 cm or 33.5 × 33.5 cm depending on cage dimensions) and mounted on a flat board

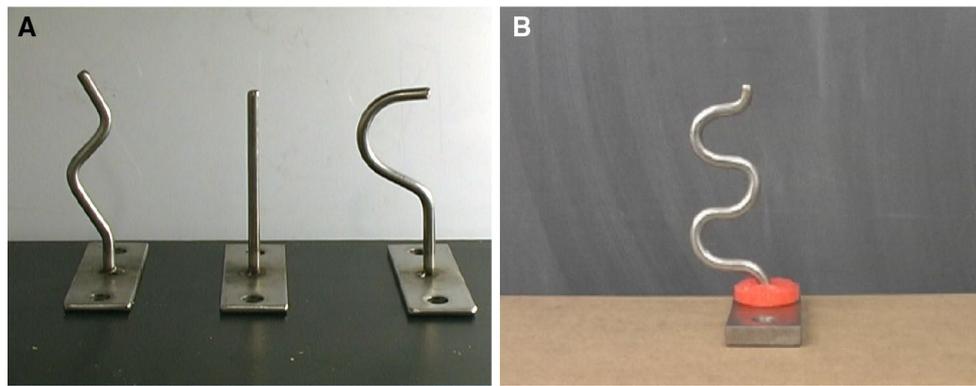


Fig. 1 Shapes used with rhesus monkeys in experiment 1. **a** The shapes used in pretraining (left to right *s*-shape, straight, question mark). **b** The novel shape used in testing (*wave*). Similar shapes were

used with chimpanzees in experiment 2. However, the shape dimensions varied to accommodate the larger hand size of chimpanzees

($7.7 \times 2.5 \times 5$ cm thick). Due to variations in housing, the apparatus was (1) mounted to the door opening of the subject's home enclosure or (2) presented at an equivalent height by placing the apparatus on a rolling cart or directly on the floor outside the subject's home enclosure. The panel had two rectangular openings (approximately 9.5×9 cm and spaced 7.5 cm apart), which allowed the monkey to insert either the left or right hand and retrieve Life Savers[®] candies from metal rods. Sliding doors on the panel allowed the experimenter to prevent access to the board as needed to control what hand the monkey used on a given trial.

Handedness groups

Monkeys completed a baseline handedness assessment for reaching prior to pretraining to establish the DOM. The door panel on the apparatus was removed, and both doors were opened. A raisin was placed between the two doors. This placement ensured that the monkey could not reach directly forward to the food, but instead had to reach around through one of the doors to retrieve the raisin. The hand used to pick up the raisin was recorded as left or right. Monkeys were given a total of 50 trials. A handedness index (HI) was calculated for each monkey using the formula $(R - L) / (R + L)$, where R was the total number of right hand reaches and L was the total number of left hand reaches. HI values range from -1.00 (exclusive left-hand use) to 1.00 (exclusive right-hand use). Negative values were considered left-handed, and positive values were considered right-handed for analyses. Seven monkeys were classified as left-handed, and six monkeys were classified as right-handed.

Shape pretraining

Monkeys were familiarized to the task of removing a Life Savers[®] candy (2.5 cm diameter) from a metal rod

(7.5×2.5 cm) bolted to the platform of the apparatus using three different training shapes (straight rod, *s*-shaped rod, and question mark-shaped rod; Fig. 1a). Monkeys completed six trials per session, attempting each shape with each hand in a randomized order, until they reached criterion of removing the candy twice with each hand in two consecutive sessions. If the monkey attempted to use the contralateral hand, the experimenter closed the doors on the apparatus and restarted the trial. Thus, after pretraining, monkeys had learned that the goal of the task was to remove the Life Savers[®] with the hand ipsilateral to the rod.

Novel shape testing

Unlike the pretraining trials where hand use was mixed throughout a session, testing for the novel rod shape ($8.0 \times .5 \times 2.5$ cm wave-shaped rod; Fig. 1b) consisted of six trials with a single hand until the monkey reached criterion. Criterion was set at removing the candy in under 15 s in 10 out of 12 trials over two consecutive sessions. The opening of the rod was always set to face out for consistency in task difficulty. Monkeys were randomly assigned to start with either their left hand or their right hand, thus creating four test groups (Table 1). Six monkeys began the novel shape testing with the DOM, and seven began with their NDOM. Trials were timed with a stopwatch, and exact latencies to remove the Life Savers[®] candy were verified through frame-by-frame coding from videotape. A trial ended when the monkey successfully removed the candy, removed their hand from the apparatus, or a maximum time of 60 s had elapsed.

Data analysis

T tests were used to examine the effects of order (trained versus untrained hand), hand (left or right), and hand

Table 1 Number of subjects by handedness group and starting hand for monkeys (experiment 1) and chimpanzees (experiment 2)

	Monkeys ($N = 13$)		Chimpanzees ($N = 52$)	
	Left-handed	Right-handed	Left-handed	Right-handed
Start left hand	3	3	10	15
Start right hand	4	3	6	21

preference (DOM or NDOM) on mean latency to solve the task in the first session with each hand. If the monkey did not solve the trial, they were given the maximum time of 60 s. Given our question whether handedness would facilitate interhemispheric transfer on learning a motor task, a priori analyses examined handedness subgroups separately and whether they started with the DOM or NDOM independent of the direction of hand preference.

Results and discussion

Paired-samples t tests revealed a significant difference between the trained and untrained hands regardless of which hand was trained or the subject's hand preference, $t(12) = 5.729$, $p < .001$ (Table 2). The mean latency for the trained hand was 36.81 s ($SD = 12.72$), compared to 22.20 s ($SD = 9.75$) for the untrained hand. There was no difference comparing the first sessions with the left ($M = 28.59 \pm 13.67$ s) and right ($M = 30.43 \pm 12.30$ s) hands, or comparing first sessions with the DOM ($M = 28.60 \pm 13.67$ s) or NDOM ($M = 30.41 \pm 13.56$ s) hands (all $ps > .05$). When left- and right-handed monkeys were examined separately, the order effect remained significant (left-handed, $t(6) = 3.264$, $p < .05$; right-handed, $t(5) = 5.667$, $p < .01$). Thus, it appears that the direction of hand preference did not influence transfer; both handedness subgroups of the sample performed significantly

better with the second hand learning the task as opposed to the hand that learned the task initially. Moreover, starting the task with the dominant hand did not improve transfer. When subgroups were examined separately by whether they started with the DOM or the NDOM, the order effect again remained significant (start DOM, $t(5) = 3.110$, $p < .05$; start NDOM, $t(6) = 4.867$, $p < .01$; Fig. 2a). Thus, there was intermanual transfer in both directions in monkeys: DOM \rightarrow NDOM and NDOM \rightarrow DOM, supporting the prediction made by the *cross-activation* model.

Experiment 2: chimpanzees

Method

Subjects

Data were collected from 54 adult chimpanzees (*Pan troglodytes*) housed at the Yerkes National Primate Research Center (19 males; 35 females). Chimpanzees ranged in age from 9 to 53 years and included 17 mother-reared, 32 nursery-reared, and five wild caught individuals. All chimpanzees live in indoor/outdoor housing in social groups of 2–8 individuals (with the exception of one male who was singly housed by the veterinary staff for clinical and behavioral reasons). Food and water were freely available throughout the experiment. The study was conducted in accordance with the Guide for Care and Use of Laboratory Animals and complied with the Animal Welfare Act. The Emory University Institutional Animal Care and Use Committee approved the research. All chimpanzees were tested individually in their home cages on the following tasks.

Handedness groups

Previously published hand-use data from a reaching task were used to assign each individual a baseline hand

Table 2 Means and standard deviations for latency (seconds) to solve the wave shape as a function of the first session by testing order, hand, and hand preference in monkeys and chimpanzees

	Order		Hand		Hand preference	
	Start	Switch	Left	Right	DOM	NDOM
Monkeys ($N = 13$)						
M	36.81 ^a	22.20 ^a	28.59	30.42	28.60	30.41
SD	12.72	9.75	14.81	12.30	13.67	13.56
Chimpanzees ($N = 52$)						
M	5.68 ^b	4.90 ^b	5.32	5.27	5.32	5.27
SD	1.65	1.28	1.62	1.44	1.46	1.60

M mean, SD standard deviation, N number of subjects, DOM dominant hand, $NDOM$ nondominant hand

^a $p < .001$; ^b $p < .01$

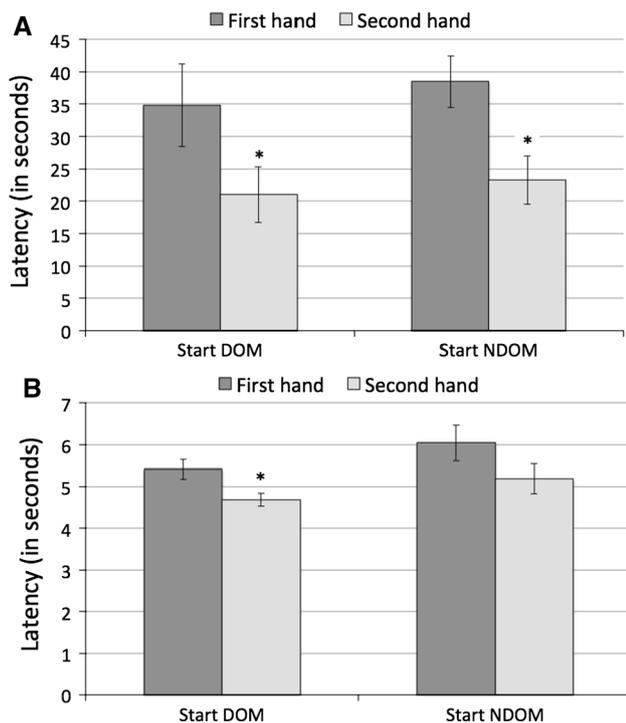


Fig. 2 Data from rhesus monkeys in experiment 1 are plotted in (a). The second hand (or untrained hand) was significantly faster than the first (trained) hand regardless of whether monkeys started with their dominant or nondominant hand. Data from chimpanzees in experiment 2 are plotted in (b). The second (untrained) hand was significantly faster than the first (trained) hand only when chimpanzees started with their dominant hand. Asterisk denotes $p < .05$

preference (Hopkins et al. 2002). In the previous study, individual raisins were thrown into the chimpanzee's enclosure and the hand used to retrieve each raisin was recorded. Subjects were required to locomote a minimum of three strides between responses to maintain postural readjustment between trials. Three subjects in the current study were not included in the original handedness study. Following the same methods described for experiment 1 in Hopkins et al. (2002), we collected 50 simple reaching responses for these individuals and categorized their hand preference based on these data. A HI was calculated for each chimpanzee using the formula given for the monkeys in experiment 1. Sixteen chimpanzees were classified as left-handed, and 36 chimpanzees were classified as right-handed. Thirty-one subjects started with the DOM, and 21 subjects started with the NDOM (Table 1). Two subjects (one male; one female) obtained an HI of .00 and were excluded from analyses because they had no clear hand preference.

Shape pretraining

Chimpanzees were familiarized to the task of removing a metal washer (2.5 cm diameter) from three

increasingly complex metal rods (straight rod: 24.1 cm long; question mark rod: 24.1 cm × 7.6 cm; or s-shape: 27.9 cm × 11.4 cm) and returning the washer to the experimenter to receive a reward (small piece of fruit or vegetable or a squirt of diluted juice). All subjects had previously been trained to the token exchange system in which an object may be exchanged for a food item. Each subject received four sessions during which the chimpanzee completed two left-hand and two right-hand trials with each rod type for a total of 12 trials. The order of presentation of the three rods was pseudo-counterbalanced across subjects and sessions, and whether each subject started with the left or right hand was counterbalanced across trials. The designated rod (with the washer in place) was inserted inside the cage horizontally, and the subject was allowed to remove the washer using the target hand. If at any point during the trial, the subject tried to use the nontarget hand or the mouth to remove the washer, the experimenter retracted the rod. The subject was not reinforced for this trial, and the trial was repeated. Thus, at the end of training, the subject had learned that the goal was to remove the washer with the hand ipsilateral to the rod and return it to the experimenter to receive a reward.

Novel shape testing

Unlike the pretraining trials where hand use was mixed throughout a session, testing for the novel rod shape (40 cm × 1.2 cm × 12 cm wave-shaped rod) consisted of 12 trials with a single hand until the chimpanzee reached criterion. Subjects only received one test session per day. Criterion was set at removing the washer in under 5 s in 10 out of 12 consecutive trials during a single session. Once the chimpanzee reached criterion with the first hand, they were tested using their other hand until reaching criterion with the second hand. The opening of the rod was always set to face away from the chimpanzee's body for consistency in task difficulty. Chimpanzees were randomly assigned to start with either their left hand or their right hand, thus creating four test groups (Table 1). Trials were timed with a stopwatch, and exact latencies to remove the washer were recorded. A trial ended when the chimpanzee successfully removed the washer.

Data analysis

Data were analyzed as in experiment 1 and examined the effects of test order (trained hand or untrained hand), hand (left or right), and hand preference (DOM or NDOM) on the mean latencies to remove the washer from the wave-shaped rod in the first session with each hand. A priori tests examined subgroups of the sample according to handedness (i.e., left-handed or right-handed) and transfer order (i.e., to or from DOM independent of handedness).

Results and discussion

There was a significant effect of order on first session latency, $t(50) = 3.644$, $p < .01$, with a mean of 5.68 s (SD = 1.65) for the trained hand and a mean of 4.90 s (SD = 1.28) for the untrained hand. There were no effects of hand (left $M = 5.32 \pm 1.62$ s; right $M = 5.27 \pm 1.44$ s) or hand preference (DOM $M = 5.32 \pm 1.46$ s; NDOM $M = 5.27 \pm 1.60$ s) on first session latency in the overall sample (both $ps > .05$).

In right-handed chimpanzees, this testing order effect remained significant, $t(34) = 3.200$, $p < .01$, with the trained hand latency (5.93 \pm 1.83 s) significantly higher than the untrained hand latency (5.00 \pm 1.40 s). In left-handed chimpanzees, however, the order effect did not hold ($p > .05$). The latency for the first hand tested (5.14 \pm 1.05 s) did not differ significantly from the second hand tested (4.69 \pm .98 s). When hand preference groups were examined independent of the direction of preference, the order effect was only significant in the subgroup of chimpanzees that trained with the preferred hand, $t(28) = 3.269$, $p < .01$ (start DOM, $M = 5.41 \pm 4.69$ s; switch to NDOM, $M = 4.69 \pm .83$ s; Fig. 2b) and did not remain significant in the other group of chimpanzees that started testing with the NDOM ($p > .05$, start NDOM, $M = 6.04 \pm 2.02$ s; switch to DOM, $M = 5.19 \pm 1.68$ s; Fig. 2b). Thus, chimpanzees differed from rhesus monkeys in that both the direction of hand preference and whether testing began with the DOM affected transfer. In left-handed chimpanzees, the mean latencies for each hand were similar during the first exposure, whereas the hands differed significantly in right-handed chimpanzees. Moreover, there was significant change in latency to solve the task, indicating intermanual transfer, in only one direction in chimpanzees: DOM \rightarrow NDOM. These patterns partially support the *proficiency* model.

General discussion

In this study, we sought to compare performance for learning a motor skill task with each hand in rhesus monkeys and chimpanzees. Subjects were randomized to train with either the DOM or NDOM based on a prior assessment of handedness. Following pretraining with differently shaped rods of increasing complexity, subjects were tested with a novel shaped rod. The test of transfer was the average latency to solve the task by removing objects from the rod in the first session with the trained hand compared to the first session with the untrained hand. Both rhesus monkeys and chimpanzees were able to perform the motor skill task, but transfer patterns differed between the two species when comparing the first session with each hand. There was no

effect of handedness on transfer in rhesus monkeys, but handedness did have an impact on transfer in chimpanzees. Our data from rhesus monkeys support the *cross-activation* model, while data from chimpanzees partially support the *proficiency* model.

The finding that there was intermanual transfer in both directions (DOM \rightarrow NDOM and NDOM \rightarrow DOM) irrespective of handedness in rhesus monkeys, but not in chimpanzees, suggests that motor information may be transferred differently in the two species. One explanation for these findings may be differences in the neurophysiology of the arm between the two species (Brinkman and Kuypers 1973). The *cross-activation* model postulates that motor engrams are formed in both hemispheres during initial hand training. This hypothesis is supported by the fact that rhesus monkeys have a greater degree of ipsilateral arm control compared to chimpanzees. For example, the right hemisphere has partial control of the shoulder and upper arm in bringing the right hand to a target. Even if only a partial engram formed in the opposite hemisphere during training via this distribution of motor control, the untrained hand would always benefit from the trained hand's experience. If this hypothesis is true, it might explain why handedness did not appear to influence transfer in monkeys. An alternative explanation for the different findings between the two species, however, may be the task itself. Due to housing variations and constraints, rhesus monkeys were tested with vertical rods, while chimpanzees were tested with horizontal rods. Additional work in other samples is needed to compare the two presentation types. Another limitation of the current study is the disparity in sample size between monkeys and chimpanzees, which reflects animal availability. Future work with a larger sample is needed to replicate the pattern found in monkeys on the intermanual transfer task.

Both direction of hand preference and the hand subjects trained with (i.e., DOM or NDOM) affected intermanual transfer in chimpanzees. Unlike rhesus monkeys, initial training with the DOM yielded a performance advantage for chimpanzees. This overall advantage from starting with the DOM is best explained by the *proficiency* model, in which the hemisphere associated with the proficient hand learns more fine motor skills and provides a model that guides the untrained hand (hemisphere) (Parlow and Kinsbourne 1989). Within handedness groups, however, this performance benefit was significant in right-handers, but not left-handers. This finding may be explained by a right-hand/left-hand hemisphere specialization for motor skills in chimpanzees. Right-hand use has been found to be associated with lower error rates on tasks requiring fine motor skills in a prior study in chimpanzees (Hopkins et al. 2002), many of whom were subjects in this report. Together, these findings of greater transfer benefits of DOM \rightarrow NDOM

with a right-hand advantage are consistent with previous studies in humans in which the left hand benefited more than the right from opposite-hand training (Halsband 1992; Laszlo et al. 1970; Mostafa et al. 2014; Parlow and Kinsbourne 1989).

As discussed in the introduction, however, this pattern of advantage for DOM \rightarrow NDOM (supporting the *proficiency* model) observed when we examined average latency for the first session of exposure with each hand differs from prior analyses on some of the chimpanzees tested here previously reported by Phillips et al. (2013). They described a transfer advantage in the opposite direction (NDOM \rightarrow DOM, supporting the *access* model) when criterion trials were used to compute a difference score as the measure of transfer. Both reports use the same task and suggest that handedness is important in understanding transfer in chimpanzees. Yet, the findings appear to be initially contradictory. We suggest that the difference can be reconciled by the fact that both the *proficiency* and the *access* models implicate that motor engrams, or motor programs, are stored in the *dominant* hemisphere during initial training. Under the *proficiency* model, motor information is stored in both hemispheres when the DOM is trained, but the DOM hand learns more skills, resulting in a performance benefit when switching to the untrained NDOM, as evidenced by shorter average latency in early trials. Likewise, under the *access* model, motor information is stored in the dominant hemisphere regardless of training hand, and a performance benefit is observed when switching to the untrained DOM, as evidenced by fewer sessions needed to reach criterion compared to the trained NDOM, because the DOM hand has direct access to motor programs. Analyzing early trials (this study) and later trials (Phillips et al. 2013 study) may provide different aspects of learning performance, and a comparison of these two methods for characterizing transfer suggests that the *proficiency* and *access* models may not be mutually exclusive. Future work is needed using imaging techniques to characterize where motor programs are stored and accessed during learning, and to elucidate the mechanisms involved in interhemispheric transfer in chimpanzees as well as other nonhuman primate species.

As a first step in this effort, Phillips et al. (2013) collected magnetic resonance and diffusion tensor images on a subset of the chimpanzees reported on here and examined the relationship between behavioral patterns of transfer and corpus callosal microstructure. Greater transfer was associated with lower fractional anisotropy values or lower structural integrity in the corpus callosum. The authors hypothesized that corpus callosum structural integrity is positively associated with interhemispheric inhibition, such that lower structural integrity is linked to less interhemispheric inhibition. Less inhibition, in turn, might facilitate greater intermanual transfer.

This hypothesis was elegantly captured by Parlow and Kinsbourne (1989) who said, “(T)hat directional effects in the transfer of training between hands may be linked to brain organization, and specifically to hemispheric specialization of function, is a provocative idea” (p. 99). As evidenced both by transfer and by handedness patterns, brain organization may be different between rhesus monkeys and chimpanzees, and perhaps only chimpanzees have hemispheric specialization of motor function. To the best of our knowledge, the relationship between interhemispheric motor skill transfer and handedness has not been investigated in other nonhuman primate species, but given our results, warrants further investigation, particularly in populations for which a left-hand bias predominates. Future work is needed to better model interhemispheric transfer in primates across a variety of intermanual tasks.

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