Handedness Influences Intermanual Transfer in Chimpanzees *(Pan troglodytes)* but not Rhesus Monkeys *(Macaca mulatta)*

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Background

- **Intermanual transfer** refers to an effect whereby training one hand to perform a motor task improves performance in the opposite untrained hand (e.g., Schulze, 2002).
- We tested the hypothesis that handedness facilitates transfer in two nonhuman primate species: rhesus monkeys and chimpanzees.
- We chose these model species because (1) they differ in the motor control of the arms and (2) they differ in the distribution and direction of handedness.
  - Rhesus monkeys have greater ipsilateral control of the upper arm and shoulder compared to chimpanzees (Brinkman & Kuypers, 1973; Kuypers, 1982).
  - Handedness in rhesus monkeys has been equivocal (c.f., Bennett et al., 2008). By contrast, there is substantial evidence for population-level right-handedness in chimpanzees (e.g., Hopkins et al., 2011).
- Given theses neurobehavioral differences, we expected that handedness would affect transfer in chimpanzees, but not monkeys.
- In the transfer task, subjects removed a Life Savers® candy (rhesus monkeys) or a washer (chimpanzees) from metal shapes (**Fig. 2**). Data were collected from both hands in a 2 x 2 (Handedness: left-handed or right-handed x Training: start dominant (DOM) or non-dominant (NDOM) hand (**See Methods**).
- Hypotheses were derived from three models of transfer (Taylor & Heilman, 1980; Parlow & Kinsbourne, 1989): *Access*: benefit training with the non-dominant hand; p*roficiency*: benefit training with the dominant hand; and *cross-activation*: benefit irrespective of training hand.
  - We predicted that hand transfer patterns in rhesus monkeys would support the *cross-activation* model whereas transfer patterns in chimpanzees would support either the *access* or *proficiency* models of transfer.

Methods

- **Subjects**
  - 13 adult rhesus monkeys housed at the University of Massachusetts Amherst (8 males; 5 females).
  - 52 adult chimpanzees housed at the Yerkes National Primate Research Center (18 males; 34 females).
- **Handedness Groups**
  - The hand used for simple reaching was recorded for 50 trials. A Handedness Index (HI) was computed for each subject, *HI = (# Right – # Left)/Total*. Positive HI scores were considered right-handed and negative scores left-handed. See **Table 1** for a distribution of subjects across handedness groups by species.

Table 1. Number of subjects by handedness group and starting hand by species.

	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

- **Shape Pre-Training**
  - Subjects were trained to remove a candy or a washer (exchanged for a treat) from three simple rods (**Fig. 1**).

Figure 1. Rods used in monkey pre-training from left to right: S-shaped, straight, question-mark. Chimpanzees received the same three shapes in pre-training but rods were larger and presented horizontally.

- **Test of Transfer**
  - Transfer was measured by latency by comparing the average time taken to solve the task using a novel rod (**Fig. 2**) in the first session with the training hand compared to the first session with the untrained hand. Training was complete when subjects met a time criterion over two consecutive test sessions.

Figure 2. Novel wave-shaped rod used in test of transfer. Picture depicts monkey setup with a Life Savers® candy. Chimpanzees removed a washer and exchanged it for a treat.

Results

- **Rhesus Monkeys**
  - Intermanual transfer (i.e., shorter latency in the untrained hand) occurred whether monkeys trained with the DOM or NDOM (**Fig. 3**), or whether monkeys were left-handed or right-handed.

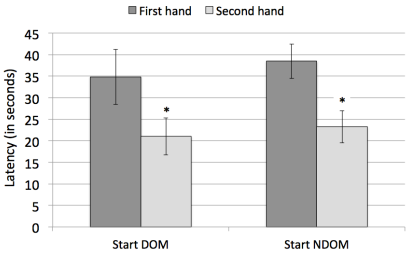

Figure 3. Data from rhesus monkeys. The second (untrained) hand was significantly faster than the first hand regardless of whether training occurred with the DOM, $t(5) = 3.110$, $p < .05$, or the NDOM, $t(6) = 4.867$, $p < .01$.

- **Chimpanzees**
  - Intermanual transfer was unidirectional, occurring only when training occurred with the DOM in chimpanzees (**Fig. 4**).

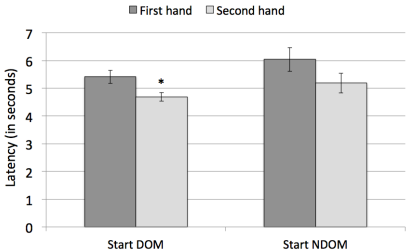

Figure 3. Data from chimpanzees. The second (untrained) hand was significantly faster than the first hand only when chimpanzees trained with the DOM, $t(28) = 3.269$, $p < .05$. There was no difference in latency between the two hands when the NDOM was trained ($p > .05$).

  - When handedness groups were analyzed separately, transfer was only observed in right-handed chimpanzees, $t(34) = 3.200$, $p < .01$. The trained and untrained hands did not differ in left-handers ($p > .05$).

Discussion

- Data from rhesus monkeys support the *cross-activation* model because a benefit occurred independent of which hand (DOM or NDOM) was trained. The untrained hand was always faster to solve the task.
- Data from chimpanzees partially support the *proficiency* model because a benefit occurred only when the DOM was trained. However, this pattern only held for right-handers when handedness subgroups were examined.
- The finding that there was transfer in both directions (DOM->NDOM and NDOM->DOM) regardless of handedness in rhesus monkeys but not in chimpanzees suggests that motor information may be transferred differently in the two species.
- Future work that utilizes imaging techniques is needed to characterize where motor programs are stored and accessed during learning, and to elucidate the mechanisms involved in intermanual transfer in primates.
- **Conclusion:** As evidenced by transfer and handedness patterns, brain organization may differ between monkeys and chimpanzees. Perhaps only chimpanzees have hemispheric specialization of motor function.

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