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CHIMPANZEE RIGHT-HANDEDNESS: INTERNAL AND EXTERNAL VALIDITY IN THE ASSESSMENT OF HAND USE

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Introduction

Recent studies in captive and wild monkeys and apes have documented evidence of population-level handedness (see Bradshaw and Rogers, 1993; Ward and Hopkins, 1993). Similarly, population-level limb preferences have been reported in other vertebrates (Rogers and Andrew, 2002). Despite the increasing evidence of population-level asymmetries in vertebrates, there remain many skeptics of these findings and the criticisms have been both methodological and statistical (Crow, 2004; McGrew and Marchant, 1997; Palmer, 2002, 2003). Interestingly, the nature of many of these criticisms was subject to discussion in the recent reviews of Annett's (2002) book on handedness in this journal (see commentaries by Corballis (2004) and Elias (2004). Annett (2004) herself claimed that she was skeptical of the evidence of handedness in chimpanzees, particularly from my laboratory. In this paper, I address some of the criticisms of our work.

Internal and External Validity in Hand Use

In 1995, I reported evidence of population-level right handedness for a measure referred to as the TUBE task (Hopkins, 1995). The TUBE task assesses hand use for coordinated bimanual actions. Briefly, peanut butter is placed on the inside edges of a poly-vinyl-chloride pipe that is approximately 2.5 cm in diameter and approximately 20 to 25 cm long. The PVC is handed to the subjects and they hold the pipe with one hand and extract the peanut butter with a finger from the opposite hand. The hand of the finger used to extract the peanut butter is recorded as the dominant hand. The original study was criticized on several grounds including a) a lack of control for which hand the subjects took the TUBE with and b) we recorded each probing actions as an individual response rather than record bouts of hand use (McGrew and Marchant, 1997) and c) unequal number of observations of hand use across subjects (Palmer, 2002) and d) the results were restricted to the colony of chimpanzees housed at the Yerkes National Primate Research Center (Palmer, 2002, 2003). Shown in Figure 1 are the mean handedness indices for several follow-up studies on the TUBE task. Neither controlling for which hand takes the TUBE (Hopkins et al., 2001), controlling the number of responses obtained from each chimpanzee (Hopkins and Cantalupo, 2003) nor recording bouts rather than individual responses (Hopkins et al., 2005a) altered the general conclusion of population-level right handedness for this task. Furthermore, evidence of population-level right handedness was not restricted to the Yerkes chimpanzees but evident in two additional colonies of captive chimpanzees (Hopkins et al., 2004). Lastly, consistency in hand use between colonies was not restricted to the TUBE task (see Figure 2). We have found consistent patterns of hand use

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between two colonies of chimpanzees for four additional measures including manual gestures, simple reaching and tool use (Hopkins et al., 2005b, 2005c).

Discussion

The results of our studies indicate that captive chimpanzees show population-level right handedness. Contrary to some claims, these results are not restricted to the YERKES colony nor can these results be explained on the basis of the subject's human rearing experience. Notwithstanding, the issue of discrepant findings between wild populations of apes compared to our studies in captive chimpanzees remains an important issue. I believe there are several possible explanations for this discrepancy.

First, in studies of captive chimpanzees, we have much greater control over positional and situational factors, which stands in strong contrast to the observation conditions in wild chimpanzees (Hopkins and Cantalupo, 2004). Having better control of these variables may allow for more robust expressions of population-level handedness in captive compared to wild chimpanzees. I believe that measuring handedness for tasks that require coordinated bimanual actions, such as the TUBE task, greatly enhance the probability of detecting population-level handedness in captive and wild chimpanzees and other great apes (see Byrne and Byrne, 1991; Corp and Byrne, 2004; Colell et al., 1995; Hopkins and Rabinowitz, 1997; Hopkins et al., 2003). Second, the behaviors measured and sensitivity of these measures differ substantially between studies in wild and captive chimpanzee. With the exception of tool use, most measures of hand use in wild chimpanzees do not elicit hand preferences at the individual level (i.e., subjects do not show lateralized preferences) (see Marchant and McGrew, 1996; McGrew and Marchant, 2001). In contrast, most structured measures used in captive studies of chimpanzee do elicit significant hand preferences at the individual level. Thus, there are differences in the sensitivity of handedness measures between settings. The exception is tool use, where strong individual preferences are elicited in both captive and wild chimpanzees (see Boesch, 1991; McGrew and Marchant, 1992; McGrew et al., 1999; Sugiyama, 1995; Sugiyama et al., 1993). Interestingly, both captive and wild chimpanzees do not show population-level handedness for tool use (see Lonsdorf and Hopkins, 2005), suggesting consistency not discrepancy in findings. Third, the effect sizes for handedness are weak to moderate in our captive subjects (Cohen's $d = .40$) but we can detect this effect because of relatively large samples of subjects in our studies. In contrast, samples sizes in wild chimpanzees (and other apes) are much smaller and, arguably, too small to detect the moderate effect observed in captive populations. Lastly, all caveats aside, there is some evidence of population-level right handedness in wild chimpanzees but they have been down played in the literature (see Hopkins and Cantalupo, 2004). For example, Boesch (1991) measured handedness for reaching, grooming, wodge dipping (a form of tool use) and nut-cracking (another tool use task). If a one sample t-test is applied to the percentages right hand use for each measure observed by Boesch (1991), the chimpanzees do show population-level right handedness for grooming and wodge dipping.

In sum, I would argue that captive chimpanzees and other great apes exhibit population-level handedness. More systematic and controlled studies are needed in wild apes before any definitive statements can be made regarding the potential role of different settings on the expression of handedness. An important finding, to which the comparative method can offer some interesting insight, is the difference in distribution of handedness between apes and humans. The ratio of right- to left-handed chimpanzees is about 2 : 1 or 3 : 1 (in the case of gesture and throwing) which is lower than most reports of handedness in various human cultures (Raymond and Pontier, 2004). Whether this difference reflects the emergence of socio-cultural evolution or alterations in the genome between chimpanzees and humans remains unknown but warrants further investigation.

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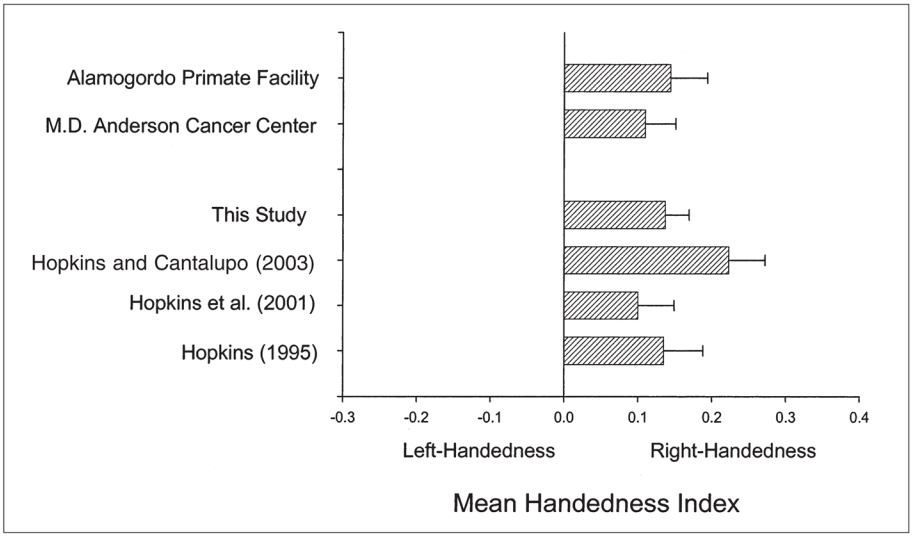

Fig. 1.

Mean handedness index (+ s. e.) for several studies using the TUBE task in captive chimpanzees. Handedness indices are calculated following the formula [H = (#R−#L)/(#R +#L)] where R and L refer to the number of left and right hand responses (Reprinted by Hopkins et al., 2005a).

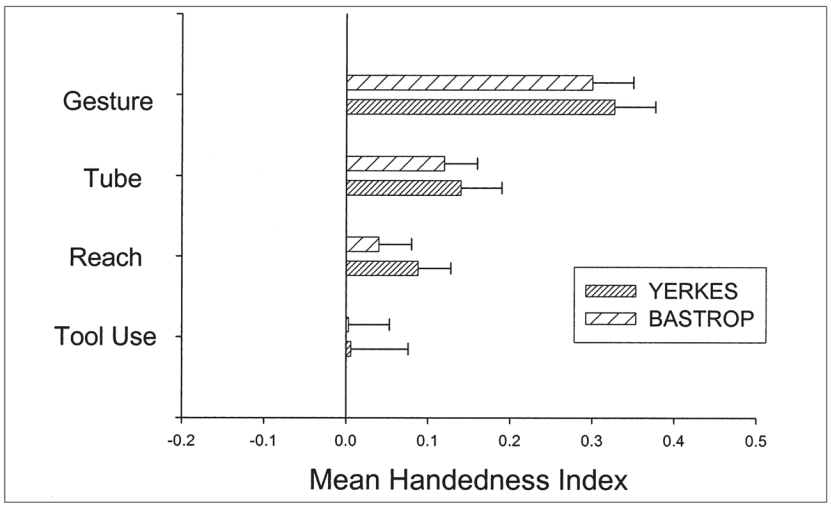

Fig. 2.
Mean handedness index (+ s. e.) for 4 behavioral measures collected in the YERKES and BASTROP chimpanzees colonies. As can be seen, HI scores were comparable across measures and colonies.